TROPHIC DYNAMICS IN A CHANGING ARCTIC: INTERACTIONS BETWEEN PTARMIGAN AND WILLOWS IN NORTHERN ALASKA

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TROPHIC DYNAMICS IN A CHANGING ARCTIC: INTERACTIONS BETWEEN PTARMIGAN AND WILLOWS IN NORTHERN ALASKA

A

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Abstract

Shrubs have been expanding in the Arctic over the past century, with important consequences for ecosystem functioning, plant community composition, and wildlife habitat. Herbivores have the capacity to strongly moderate the growth and biomass of shrubs, and therefore need to be considered when attempting to understand and project future changes to Arctic ecosystems. Ptarmigan (*Lagopus lagopus, L. muta*) are common and widespread in many tundra regions, and feed on shrubs throughout their life cycle. Ptarmigan are likely to be an important herbivore in northern Alaska where shrub expansion is rapidly occurring; however, little is known about their spatial and temporal distribution in the Arctic, or the effect of their browsing on shrubs. This dissertation provides novel information on ptarmigan population ecology and herbivory in northern Alaska.

Ptarmigan occupancy in northeastern Alaska increased from March through May, lending support to the idea that they undergo a spring migration from southern wintering grounds to breeding grounds north of the Brooks Range. Ptarmigan distributions were strongly linked to the presence of shrubs; occupancy was greatest in dense patches of riparian willows that grew tall enough to exceed snow depth.

The frequency and intensity of ptarmigan browsing in feltleaf willow (*Salix alaxensis*) stands in northeastern and northwestern Alaska was high, such that ptarmigan browsed 82-89% of willows and removed 30-39% of buds. Browsed willow branches produced fewer catkins than un-browsed branches, but doubled the volume of current annual growth produced the following summer. These longer, larger-diameter shoots bore 40-60% more buds than shoots on un-browsed branches. The removal of distal buds stimulated dormant buds at the base of the branch to produce shoots, resulting in a "broomed" architecture. Despite their tendency to produce

longer shoots when browsed, highly broomed willows with a history of browsing were shorter than un-broomed willows. Broomed willows were more likely to be re-browsed by ptarmigan. Moose browsing was not as prevalent (17-44% of willows browsed) as ptarmigan browsing and resulted in reduced catkin production and increased shoot volume.

Simulated ptarmigan browsing of feltleaf willows caused a similar response to that observed in the wild. Browsed willows produced fewer catkins and more buds per shoot, although buds were smaller than on un-browsed willows. Browsing altered the architecture and bud production of willows such that the biomass of easily accessible buds (within 50 cm of snow level) was greater (129 ± 30 mg) on browsed willows than un-browsed willows (113 ± 50 mg). Browsing did not affect nitrogen concentrations, but slightly reduced carbon concentrations and protein precipitation capacity (tannins) in buds produced the following winter. In a feeding preference study, when broomed and un-broomed willow branches were placed in the snow at equal heights, wild ptarmigan showed no preference for either type but obtained more buds from broomed willows.

A synthesis of original and published research showed that browsing by vertebrate herbivores in the Arctic is not uniform, and that certain shrubs (such as willows) are more heavily browsed than others (such as evergreen ericoids, resin birches, and Siberian alder (*Alnus viridis fruticosa*)). These differences in preference translate to variation in the degree to which herbivores regulate Arctic shrub growth and community structure. As shrubs expand in the Arctic, unpalatable, fast-growing species such as alder may have an advantage over more palatable species such as willows. Collectively, this research fills critical gaps in our knowledge of ptarmigan population ecology in Alaska, provides novel insights into how ptarmigan regulate

their food source for their own benefit, and enhances our understanding of how herbivores influence shrub expansion in the Arctic.

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Chapter 1

General Introduction

The Arctic is experiencing rapid warming compared to other parts of the world (Collins et al. 2013), and dramatic changes to Arctic vegetation have been observed over the past century. One of the most obvious and quantifiable changes has been the expansion of woody shrubs (Sturm et al. 2001; Tape et al. 2006; Frost and Epstein 2014). Shrub expansion influences the distribution of herbivores that depend on shrubs for food and cover from predators. In turn, herbivores may act as moderators of the ongoing shrub expansion due to their ability to profoundly influence the plants they forage on (Myers-Smith et al. 2011).

Arctic herbivores such as caribou and reindeer (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), ptarmigan (*Lagopus lagopus*), and voles (*Clethrionomys rufucanus)* can reduce the height, growth, and biomass of woody shrubs (Crete and Doucet 1998; Hakkarainen et al. 2007; Gough et al. 2007; Dahlgren et al. 2007; den Herder et al. 2008; Pajunen et al. 2012; Zamin and Grogan 2013) and in some cases inhibit the expansion of shrubs under warmer conditions (Post and Pedersen 2008; Olofsson et al. 2009). Thus, foraging preferences by Arctic herbivores can influence the dynamics of shrub expansion, significantly reducing the biomass of palatable species while giving less preferred species a competitive advantage (Butler and Kielland 2008; Zamin and Grogan 2013).

Conversely, herbivores do not always reduce the biomass of their forage plants, instead increasing plant productivity, accessibility, and quality by inducing a compensatory growth

response (Hilbert et al. 1981; McNaughton 1983; Du Toit et al. 1990; Stewart et al. 2006). By creating and maintaining "grazing lawns", aggregations of herbivores can increase the carrying capacity of their own habitat (McNaughton 1984). Fertilization via urine and feces (Ruess et al. 1989), combined with translocation of resources within plant tissues facilitates this process (Holland and Detling 1990). Optimal conditions in which herbivory causes a compensatory response are: a) the plant has adequate access to resources such as light, water, and nutrients (Wise and Abrahamson 2007; Maschinski and Whitham 2011), b) the herbivore applies low to moderate rather than severe browsing pressure (Hilbert et al. 1981), and c) the plant population exhibits "tolerance" traits (e.g. fast-growing, poorly-defended, and adapted to disturbance (Coley et al. 1985; Herms and Mattson 1992).

An important goal of this dissertation is to apply the above theories to ptarmigan-willow interactions in northern Alaska and to determine whether ptarmigan limit the growth and reproduction of feltleaf willows (*Salix alaxensis*) and therefore inhibit their expansion, or instead have no effect on or even enhance the productivity of this species, which is highly tolerant of herbivory.

Ptarmigan (*L. lagopus, L. muta*) are ubiquitous but often overlooked Arctic herbivores that may play a significant role in Arctic shrub ecosystems because they specialize on the buds of willows (*Salix* spp.) and birch (*B. nana*) in the winter and spring (Irving et al. 1967; Weeden 1969). By removing terminal buds from willow branches that grow tall enough to exceed snow depth, ptarmigan appear to create "hedges" of willows above snow line (Hakkarainen et al. 2007; Tape et al. 2010). Consequently, ptarmigan may limit the expansion of shrubs by pruning them, while

simultaneously increasing the number of buds within easy reach in future years. Determining the potential for ptarmigan regulation of willow expansion is therefore important for understanding habitat change in a warming Arctic.

Chapter 2 of this dissertation addresses gaps in our knowledge of ptarmigan distribution and seasonal movements in northern Alaska. Despite their abundance and ecological role in Arctic Alaska, no detailed studies have been conducted on ptarmigan since the 1960's (Weeden 1964; Irving et al. 1966; West and Meng 1966; Irving et al. 1967; Weeden 1969). My goal was to evaluate whether ptarmigan continue to migrate across the Brooks Range in the spring, as observed by Irving et al. (1966), and to quantify the relationship between ptarmigan occupancy and shrub cover. We conducted aerial surveys of ptarmigan and their habitat in the spring of 2011 and 2012 and used multi-seasonal occupancy models to test whether ptarmigan occupancy varied within and among years, and the degree to which colonization and extinction probabilities were related to shrub cover and latitude.

The widespread distribution and close association between ptarmigan and shrub patches in the Arctic suggest that ptarmigan may play a major role in moderating shrub expansion. In chapter 3, we quantify the effect of browsing by ptarmigan and another important Arctic herbivore, moose (*Alces alces*), on early successional feltleaf willows. We focus on feltleaf willows because they are preferred by ptarmigan and moose in the winter and spring, and are one of the few shrub species available for browsing at that time (Weeden 1969; Risenhoover 1989). First, we quantified the frequency and intensity of ptarmigan and moose browsing on feltleaf willows at sites in northern Alaska. Then, we used stage-structured population models to determine how

survival and production of new buds differed between browsed and un-browsed willows, leading to differences in bud abundance, shoot and catkin production, and plant architecture.

To complement chapter 3, which was an observational study of how browsed and un-browsed willows differed, we simulated browsing on feltleaf willows inside an exclosure with all variables other than browsing controlled. Chapter 4 describes the results of this study, and uncovers the mechanisms by which ptarmigan influence the growth, reproduction, and architecture of willows. Additionally, we tested whether ptarmigan browsing increased the nutritional value of willow buds by decreasing the concentrations of secondary metabolites. Lastly, we conducted a feeding preference study with wild ptarmigan to test whether they showed a preference for or obtained more food from broomed (with a history of browsing) versus un-broomed willow branches. In combination, these experiments effectively test whether ptarmigan enhance the abundance, quality, and accessibility of their food resource.

Chapter 5 of this dissertation synthesizes new and existing research on how vertebrate herbivores influence expanding shrub communities in the Arctic. Many recent studies have examined the importance of top-down regulation of shrub growth by herbivores, which varies by shrub species and functional group. Deciduous shrubs tend to be faster-growing and respond more quickly to improved conditions (e.g. longer growing seasons, greater soil nutrient availability) in the Arctic, yet they are preferred by herbivores and may be outcompeted by less palatable evergreen shrubs at high levels of browsing intensity. To synthesize the current understanding of top-down regulation of shrubs in the Arctic, we collected evidence from multiple observational and

experimental studies to evaluate the degree to which different shrub species are regulated by herbivores in Arctic ecosystems.

1.1 References

Butler LG, Kielland K (2008) Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. J Ecol 96:136–144. doi: 10.1111/j.1365-2745.2007.0

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 235:895–899.

Collins M, Knutti R, Arblaster J, et al. (2013) Long-term climate change: Projections, commitments and irreversibility. Clim. Chang. 2013 Phys. Sci. Basis. Contrib. Work. Gr. I to Fifth Assess. Rep. Intergov. Panel Clim. Chang.

Crete M, Doucet GJ (1998) Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. Arct Alp Res 30:126–132.

Dahlgren J, Oksanen L, Sjödin M, Olofsson J (2007) Interactions between gray-sided voles (*Clethrionomys rufucanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. Oecologia 152:525–32. doi: 10.1007/s00442-007-0664-8

Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Glob Chang Biol 20:1264–77. doi: 10.1111/gcb.12406

Gough L, Ramsey EA, Johnson DR (2007) Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Oikos 116:407–418. doi: 10.1111/j.2007.0030-1299.15449.x

Hakkarainen H, Virtanen R, Honkanen JO, Roininen H (2007) Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biol 30:619–624. doi: 10.1007/s00300-006-0221-7

den Herder M, Virtanen R, Roininen H (2008) Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic Appl Ecol 9:324–331. doi: 10.1016/j.baae.2007.03.005

Herms D, Mattson WJ (1992) The dilemma of plants: To grow or defend. Q Rev Biol 67:283. doi: 10.1086/417659

Hilbert ADW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Irving L, West C, Peyton LJ, Paneak S (1966) Migration of willow ptarmigan in arctic Alaska. Arctic 20:77–85.

Irving L, West GC, Peyton LJ (1967) Winter feeding program of Alaska willow ptarmigan shown by crop contents. Condor 69:69–77.

Maschinski J, Whitham T (2011) The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. Am Nat 134:1–19.

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886.

Myers-Smith IH, Forbes BC, Wilmking M, et al. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:610–623. doi: 10.1088/1748-9326/6/4/045509

Olofsson J, Oksanen L, Callaghan T, et al. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. Glob Chang Biol 15:2681–2693. doi: 10.1111/j.1365-2486.2009.01935.x

Pajunen A, Virtanen R, Roininen H (2012) Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. Oikos 121:1544–1552. doi: 10.1111/j.1600-0706.2011.20115.x

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci USA 105:12353–12358. doi: 10.1073/pnas.0802421105

Risenhoover KL (1989) Composition and quality of moose winter diets in interior Alaska. J Wildl Manage 53:568–577.

Ruess RW, Hik DS, Jefferies RL (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23–29.

Stewart KM, Bowyer RT, Ruess RW, et al. (2006) Herbivore optimization by North American elk: consequences for theory and management. Wildl Monogr 167:1–24.

Sturm M, Racine C, Tape K, et al. (2001) Increasing shrub abundance in the Arctic. Nature 411:2001–2002.

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in northern Alaska and the Pan-Arctic. Glob Chang Biol 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186–193. doi: 10.2980/17-2-3323

Du Toit JT, Bryant JP, Frisby K (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71:149–154.

Weeden R (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

Weeden RB (1964) Spatial separation of sexes in Rock and Willow Ptarmigan in winter. Auk 81:534–541.

West G, Meng M (1966) Nutrition of willow ptarmigan in northern Alaska. Auk 83:603–615.

Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: A review and assessment of three opposing models. Am Nat 169:443–54. doi: 10.1086/512044

Zamin TJ, Grogan P (2013) Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. J Ecol 101:671–683. doi: 10.1111/1365-2745.12082

Chapter 2

Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic[1]

2.1 Abstract

Rock and willow ptarmigan are abundant herbivores that require shrub habitats in Arctic and alpine areas. Shrub expansion is likely to increase winter habitat availability for ptarmigan, which in turn influence shrub architecture and growth through browsing. Despite their ecological role in the Arctic, the distribution and movement patterns of ptarmigan are not well known, particularly in northern Alaska where shrub expansion is occurring. We used multi-season occupancy models to test whether ptarmigan occupancy varied within and among years, and the degree to which colonization and extinction probabilities were related to shrub cover and latitude. Aerial surveys were conducted from March to May in 2011 and April to May 2012 in a 21230 km^2 area in northeastern Alaska. In areas with at least 30% shrub cover, the probability of colonization by ptarmigan was >0.90, indicating that patches of shrubs associated with riparian areas had a high probability of becoming occupied by ptarmigan. Occupancy increased throughout the spring in both years, providing evidence that ptarmigan migrated from southern wintering areas to breeding areas north of the Brooks Range. Occupancy was higher in the moderate snow year than the high snow year, and this was likely due to higher shrub cover in the moderate snow year. Ptarmigan distribution and migration in the Arctic are linked to expanding shrub communities on a wide geographic scale and these relationships may be shaping ptarmigan population dynamics, as well as rates and patterns of shrub expansion.

[1]Christie, KS, MS Lindberg, RW Ruess, and JA Schmutz. 2014. Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. Polar Biology DOI: 10.1007/s00300-014-1504-z

2.2 Introduction

Climatic warming in the Arctic has resulted in the rapid expansion of woody shrubs over the past half-century (Chapin et al. 1995; Sturm et al. 2001; Walker et al. 2006; Tape et al. 2006). Shrub expansion in Arctic tundra ecosystems has been compared to the melting of sea ice because shrubs are dark objects on the landscape that lower ground surface albedo, absorb heat, and accelerate snowmelt, thus creating a positive-feedback to climate warming (Sturm et al. 2005). Rapidly expanding shrubs in the Arctic will likely change the distributions of wildlife, and one might expect to observe range contractions of tundra-adapted species and range expansion of shrub-adapted species. Willow (*Lagopus lagopus*) and rock ptarmigan (*L. muta*) require shrubs tall enough to exceed snow depth for food and protection in the winter, and therefore may benefit from the ongoing shrub expansion at this time. During the summer, however, the habitat requirements of the two species diverge: willow ptarmigan depend upon shrub thickets for breeding habitat, whereas rock ptarmigan prefer more open tundra habitats (Irving et al. 1967; Hannon et al. 1998; Montgomerie and Holder 2008; Ehrich et al. 2012). Shrub expansion may therefore increase winter habitat for both species but reduce the extent of tundra breeding habitat for rock ptarmigan.

While possibly benefiting from climate-induced changes to their habitat, ptarmigan may in turn be interacting with climate to influence their forage plants. Rock and willow ptarmigan may have a disproportionately large effect on the Arctic landscape of North America, given their small body size. Dominant Arctic shrubs, such as willows (*Salix alaxensis, S. pulchra, S. lanata, S. arbusculoides*) and dwarf birch (*Betula glandulosa, B. nana.)* are extensively browsed by

ptarmigan, who remove the terminal buds and strip the bark of shoots grown the previous summer (Weeden 1969; Williams et al. 1980; Tape et al. 2010). Willows are particularly important for willow ptarmigan, whose diet is composed of 62-91% *Salix* spp. from October through May (Weeden 1969). In northern Alaska, up to 90% of all buds were removed from *Salix alaxensis* branches by ptarmigan (Tape et al. 2010).The removal of buds by ptarmigan reduces height, increases architectural complexity, and reduces catkin production (Hakkarainen et al. 2007). The result is a stunted, "hedged" appearance of many willows across Arctic Alaska (Tape et al. 2010).

Despite their prevalence and ecological role in northern Alaska, little is known about the movements of ptarmigan in this region, and the last detailed studies occurred in the 1960's (Weeden 1964; Irving et al. 1966; West and Meng 1966; Irving et al. 1967). Arctic-breeding rock and willow ptarmigan were observed to migrate south of the Brooks Range for the winter months by Irving et al. (1966). These authors recorded annual migrations of large numbers (>50,000 birds) of ptarmigan through the Brooks Range and noted that Arctic-breeding females and juveniles tended to move farther south during winter than did adult males. This phenomenon of sexual segregation during the winter months has been observed in ptarmigan populations elsewhere (Weeden 1964; Gruys 1993; Schwab et al. 2005). Rock and willow ptarmigan migration distance is variable, ranging from zero to 160 km (Jenkins et al. 1963; Weeden 1964; Gruys 1993). Gardarsson and Moss (1970) and Bergerud and Gratson (1988) hypothesized that greater food availability and cover from predators in wintering areas drives female and juvenile ptarmigan to migrate, whereas males are under greater selective pressure to remain near breeding grounds and defend territories. Mossop (1988) found that female willow ptarmigan in British

Columbia traveled shorter distances from breeding grounds in years of moderate snow cover, indicating that migration distance is flexible, and is dictated by the search for food and cover from predators. Ptarmigan therefore appear to move only as far as necessary to obtain adequate food and shelter (Johnsgard 1973). With expanding shrubs in a warmer climate, one logical prediction is that the need to migrate would diminish, and more ptarmigan would over-winter near their Arctic breeding grounds. It is possible that a half century after the migration of ptarmigan was described by Irving et al. (1966), shrub expansion has created an environment where Arctic ptarmigan are no longer under strong selective pressure to migrate.

An important step in determining how ptarmigan are influenced by shrubs, and in turn influence shrub expansion in Arctic Alaska, is to understand their distribution and migration. We tested several hypotheses regarding ptarmigan distribution and movement patterns using multi-season occupancy models (Table 1, Mackenzie et al. 2006). First, we evaluated whether changes in distributions of ptarmigan provide evidence for a spring migration to northern Alaska in 2011 and 2012 by comparing a model specifying constant occupancy in March, April and May to models allowing occupancy to change across months (Mackenzie et al. 2006, Table 1). Second, we tested if patch occupancy was dependent on whether the patch was previously occupied, i.e., did the population exhibit "Markovian dynamics" (Mackenzie et al. 2006). Third, we tested whether colonization and extinction probabilities were dependent on percent shrub cover and/or latitude. Colonization was defined as the probability that a previously unoccupied unit became occupied the subsequent survey, and extinction was the probability that a previously occupied unit became unoccupied. We predicted that the probability of colonization would be highest and extinction lowest in extensive patches of shrubs associated with riparian areas, and areas of

snow-free ground where shorter shrubs such as dwarf birch were exposed. Furthermore, we predicted that colonization rates would be highest in southern regions of the study area early in the season, consistent with the idea that ptarmigan were migrating northward from southern wintering grounds. Lastly, we tested whether ptarmigan occupancy was higher in the year with less snow and more shrub habitat (2012) than the year of the study with heavier snowfall (2011).

2.3 Materials and Methods

Study Area

The study took place in northeastern Alaska, in the northern foothills of the Brooks Range and on the Arctic Coastal Plain. This region has experienced significant shrub expansion (Myneni et al. 1997) and supports large numbers of ptarmigan, which are thought to migrate from areas south of the Brooks Range in the spring (March-May). Tall shrubs generally occur in riparian zones around rivers and lakes, or areas with deep active layers such as thaw slumps (Schickhoff et al. 2002). Snow-free areas increase in prevalence throughout the spring, but can occur in winter on wind-swept ridges and hillsides.

Study Design

We used aerial surveys to examine spatial and temporal patterns of ptarmigan occupancy. Aerial surveys took place in a 21230 km^2 area that included a mosaic of different landscape types, including areas with tall shrubs and areas with shorter, less expansive shrub patches associated with ridges and upland tundra. Although shrubs were not identified to species, it was assumed that tall willows (*S. alaxensis, S. arbusculoides, S. lanata*) were the dominant woody shrubs in

the major river drainages, whereas alder (*Alnus viridis*), dwarf birch (*Betula nana*, *B. glandulosa*), and shorter willows (e.g. *S. glauca)* dominated upland habitats (Schickhoff et al. 2002). Our survey area was bordered to the west by the Sagavanirktok River and to the east by the Anaktuvuk River, with southernmost surveys at an approximate latitude of 68°7'N and northernmost surveys at a latitude of 69°50'N. Ptarmigan abundance and movements had previously been documented by Irving et al. (1966) at Anaktuvuk Pass, just south of our Anaktuvuk River transect. Surveys were conducted along major river drainages (the Sagavanirktok, Itkillik, and Anaktuvuk Rivers) and in randomly-located 10 X 10 km blocks. Our sampling design ensured that a range of possible habitat types were surveyed in an unbiased fashion.

To estimate ptarmigan occupancy, we conducted aerial surveys flown via fixed-wing Stinson aircraft (1948 108-3 Flying Station Wagon) on 12-15 March, 15-16 April, and 5-6 May, 2011 and on 17-18 April and 2-3 May, 2012. We did not repeat March surveys in 2012 due to low detections in March 2011, and it was determined that the migration of ptarmigan to northern Alaska begins in April, as observed by Irving et al. (1966). Our aerial surveys precluded the identification of ptarmigan to species, and we therefore refer to rock and willow ptarmigan collectively as "ptarmigan", with the expectation that willow ptarmigan may be more common in low-lying drainages due to their preference for willows, whereas rock ptarmigan may be more common in snow-free areas at higher elevations where dwarf birch is more accessible.

The study area was gridded into 10 X 10 km blocks, 6 of which were randomly chosen for aerial surveys. Random blocks were further divided into 1-km segments and were surveyed in a

systematic pattern where a 1-km segment was surveyed, followed by a 1-km segment with no observations. The 1-km segments functioned as sampling units for occupancy estimation. Within each block, five parallel transects were flown, and 22-25 segments were surveyed per block. Major river transects were surveyed continuously because we were less concerned about double counting birds along these corridors than in the random blocks, where parallel transects increased the chance of birds moving into neighboring grid cells. Sample units consisted of 1-2 km (length) by 1 km (width) segments along these transects. Each unit was surveyed once per month by two independent observers. Occupancy of ptarmigan and their tracks (presence or absence) was recorded for each sample unit. The likelihood of re-counting old tracks was minimized by the fact that it snowed between each survey (NRCS Sagwon Snotel Station). Survey duration was approximately 8 hours, and surveys were completed over two consecutive days. Surveys were only completed on days with clear skies and high visibility. The aircraft travelled at an approximate speed of 129 kph, and altitude varied from 30 m for surveys of major rivers to 61m for surveys of random blocks. The pilot was able to fly at a lower altitude along major river drainages due to their more uniform topography.

Detection probability was estimated using the double-observer method (adapted for occupancy surveys from Nichols et al. 2000), implemented in the robust design occupancy modeling framework (Mackenzie et al. 2006). Two observers were situated on the right side of the aircraft, and simultaneously observed the area within a 1000 m perpendicular distance from the aircraft. The entire survey unit was therefore on the right side of the aircraft. No communication between observers, combined with a sheet placed between the two seats ensured that observations were independent. Despite the fact that ptarmigan in winter plumage are highly cryptic on a white

landscape, it was possible to detect them due to their tendency to flush in response to the aircraft. Ptarmigan tracks were also easily discernable from heights of 30-60 m based on their unique pattern in the snow.

In addition to recording information about ptarmigan and their tracks, percent shrub cover was estimated for each sample unit. Percent shrub cover (including all shrubs tall enough to exceed snow depth and shorter shrubs in snow-free areas) was visually estimated during surveys for each sampling unit. Estimates of shrub cover were averaged between the two observers.

Analysis

Probabilities of occupancy (Ψ), colonization (γ), extinction (ε), and detection (p) were estimated using maximum likelihood estimation in program MARK (White and Burnham 1999). Two separate analyses were conducted to examine how ptarmigan occupancy changed within and across years. The first analysis (within-year) examined seasonal changes in occupancy from March through May in 2011 and April to May 2012. Initial occupancy was estimated, as well as subsequent colonization and extinction probabilities (Mackenzie et al. 2006). Within-season analyses were conducted separately for 2011 and 2012. For each year, we tested whether there was no seasonal change in occupancy and whether it exhibited non-Markovian dynamics (i.e., occupancy at time t is independent of occupancy at time t-1, where $\gamma = 1 - \varepsilon$; Table 2-1). Furthermore, we tested whether colonization and extinction rates were dependent on shrub cover and/or latitude (Table 2-1). Lastly, we tested the effect of "survey type", whether a particular survey unit was in a random block or along a major river transect. We used an information-theoretic approach to compare models, whereby models with the highest likelihood but fewest

parameters were favored. We directly compared models using the AIC weights, which reflect the weight of evidence in favor of the model, relative to all other models in the dataset (Burnham and Anderson 2002). For the across-year analysis, we tested the same hypotheses as the within-year analysis, except that we tested for changes in occupancy from 2011 to 2012 rather than within-year changes. April and May data were analyzed separately. Detection probability was modeled as a function of observer, time period (month or year), survey type, and as a constant, and the best model was used in subsequent models of occupancy.

2.4 Results

We attempted to conduct a complete survey of the study area on each survey date. However, sub-optimal weather conditions often prevented us from surveying the entire area. In 2011, we were able to survey 171 units repeatedly in March, April, and May. In 2012, we repeatedly surveyed 119 units in April and May. In both years, ptarmigan tracks were detected more frequently than birds themselves. In March 2011, no birds were detected; however, ptarmigan tracks were detected in 25% of survey units. In April 2011, birds were detected in 4% of units and ptarmigan tracks were detected in 37% of survey units. More birds were detected in May 2011, with birds and tracks detected in 14% and 57% of units, respectively. In April 2012, birds were detected in 13% of units and tracks were detected in 50% of units. The following month, birds were detected in 8% of units, whereas tracks were detected in 55% of units. Flock size was variable and ranged from 1 to 300 birds (mean = 106 birds per flock) in April and 1 to 500 birds (mean = 44 birds) in May 2011. Flock size was smaller in April 2012, ranging from 1 to 110 (mean = 15 birds), whereas in May 2012, flock size ranged from 1 to 350 (mean = 46 birds).

Within-year analysis

For the 2011 analysis, the model of detection probability (p) as a function of survey type failed to converge and therefore was not included in the set of candidate models of p. Of the remaining candidate models, the model of p as a function of month had the most support (AICc weights: month = 0.81, observer = 0.19, constant = 0.00) and was used in subsequent analyses of occupancy. For the 2012 analysis, the highest-ranked model included p as a constant (AICc weights: constant = 0.34, month = 0.24, ST = 0.24, observer = 0.18) and this parameterization was used in subsequent models of occupancy. Models specifying no seasonal change in occupancy (Ψ(March = April = May)) received no support in either year, whereas models allowing for seasonal change in occupancy (where initial occupancy is estimated and occupancy of subsequent months is derived) received substantially more support from the data (Table 2-2). The best-supported models of ptarmigan population dynamics indicated that colonization and extinction were functions of percent shrub cover and latitude (Table 2-2). For both years, the highest-ranked models were well-supported, with AICc weights greater than 0.99 (Table 2-2). Occupancy increased from March through May in 2011 and from April to May 2012, supporting the hypothesis that ptarmigan migrate to the study area from southern wintering grounds (Table 2-2, Figure 2-1). For both years, the probability that unoccupied units would be colonized the subsequent month increased with shrub cover, such that units with >30% shrub cover had a 90% chance of becoming colonized (Table 2-3, Figure 2-2,2-3). Percent shrub cover in survey units ranged from 0 to 75% and estimates were similar between observers, with correlations ranging from 0.59 to 0.77 depending on the month and year. Mean shrub cover increased from 8% in March to 9% in April to 12% in May 2011 and from 11% in April to 13% in May 2012 (Figure 2-4). In 2011, colonization increased with decreasing latitude, indicating that more southern units

had a greater chance of being colonized (Table 2-3, Figure 2-5). However, the opposite was true in 2012, at which time colonization increased with latitude (Figure 2-6). Extinction probability increased with decreasing shrub cover in both years (Table 2-2). The probability of extinction increased with latitude in 2011, but decreased with latitude in 2012 (Table 2-2).

The data supported Markovian models of ptarmigan population dynamics, indicating that the probability that a unit was occupied depended upon whether it was occupied the prior month (Table 2-2). In both years, at mean values for shrub cover and latitude, the probability of an occupied unit staying occupied the subsequent month ($1\text{-}\varepsilon_{2011} = 0.97 \pm 0.05$ (SE)), $1\text{-}\varepsilon_{2012} = 0.95 \pm 0.04$) was substantially higher than that of an unoccupied unit becoming occupied ($\gamma_{2011} = 0.41 \pm 0.07$, $\gamma_{2011} = 0.37 \pm 0.14$).

Across-year analysis

For both months, models of detection probability as a function of observer received the most support (AICc weights April: observer = 0.96, ST = 0.03, year = 0.00, constant = 0.00, May: observer = 1.00, ST = 0.00, year = 0.00, constant = 0.00), and this parameterization for detection probability was used in subsequent models of colonization and extinction Models that included effects of latitude and shrub cover on colonization and extinction received the most support for both months (Table 2-4). These models indicated that ptarmigan occupancy increased from 2011 to 2012, and the difference was most pronounced in April (Table 2-4, Figure 2-7). The effect of latitude on extinction and colonization was weak, and was estimated with low precision (Table 2-5). In April, colonization and extinction probabilities were higher at higher latitudes, whereas in May, the opposite was true (Table 2-5). Shrub cover had a positive effect on colonization

probability and a negative effect on extinction probability in both months (Table 2-5). Average shrub cover was slightly higher in 2012 than in 2011 for both months (Fig. 2-4). The Markovian models received more support than non-Markovian model in both months. Although this was the case, the probability of an occupied unit (at mean values for shrub cover and latitude) staying occupied (1-ε) the following year was similar to that of an unoccupied unit becoming occupied (γ;1-ε_{April} = 0.87 ± 0.09 , γ_{April} = 0.97 ± 0.04, 1-ε_{May} > 0.99 ± 0.00, γ_{May} > 0.99 ± 0.00).

2.5 Discussion

In this study, we found that ptarmigan in northern Alaska had a widespread, seasonally variable distribution that was closely linked to snow and shrub cover. The observed association with shrubs is consistent with recent findings by Henden et al. (2011) showing a strong relationship between ptarmigan and extensive, un-fragmented willow thickets in Fennoscandia. Our analyses revealed that ptarmigan occupancy in the study area increased during the spring months, supporting the idea that they migrate from wintering grounds south of the Brooks Range to Arctic breeding grounds. Seasonal patterns of colonization and extinction were closely related to shrub cover, which itself increased as the spring ensued. As shrubs emerged from the snow in the spring, they became available as habitat for ptarmigan at northern latitudes. This migration was first documented by Irving et al. (1966), who noted a peak in numbers of ptarmigan moving through the Brooks Range in late April, followed by a decline in May. Migration by ptarmigan is thought to be related to the search for adequate food and shelter (Bergerud and Gratson 1988), and our data suggest that shrub cover in northern Alaska is not sufficient to eliminate the need to migrate in winter. Based on Irving et al.'s observations of 10,000 birds migrating through

Anaktuvuk Pass before 7am on a single day in April, we expected to observe larger flocks of ptarmigan in the current study. The average flock size that we observed was 40 ± 10 (SE) birds, ranging from groups of one to 500. Whether this discrepancy represents a meaningful decline in overall abundance over the past 50 years, a decrease in density, or a pulse of birds moving through the study area on days that were not surveyed is unclear and merits further investigation. It is possible that with increased shrub habitat in the Arctic, ptarmigan flocks are smaller relative to historic levels, because shrub habitats are now more widespread and ptarmigan more widely dispersed across the landscape.

Ptarmigan occupancy was greater in 2012 than in 2011, and this may be due to differences in snow conditions between years. Snow depth was higher than average in 2011, with 10.2 cm of accumulated snow (water equivalent) as of 1 May, compared to the long-term average of 8.6 cm (1981-2010; NRCS Sagwon Snotel Station). Snow depth in 2012 was average, with 8.4 cm of accumulated precipitation as of 1 May. Increased occupancy in 2012 could therefore be a direct result of an increased number of sample units with suitable habitat for ptarmigan compared with the previous year. Interestingly, observers had only three ptarmigan detections in April 2011, with a mean flock size of 106 birds, whereas in April 2012 there were 19 detections, and mean flock size was 15 birds. This suggests that in the high snow year (2011), ptarmigan were concentrated in fewer available habitats compared to the moderate snow year (2012), when ptarmigan could disperse over a larger area. An alternative explanation for the observed differences in occupancy between years is cyclic changes in ptarmigan abundance, as observed elsewhere in their range (Andreev 1988; Moss and Watson 2001). No evidence was found by

Irving et al. (1966) for cyclic population dynamics in northern Alaska, but this question has not been explicitly addressed in recent years.

The time that elapsed since the last snow fall may have been positively correlated with occupancy estimates because tracks accumulate over time. In March, April, and May 2011, aerial surveys occurred within 6, 7, and 5 days of the last snow fall, respectively (NRCS – Sagwon Snotel Site). For April 2012 surveys, 12 days elapsed since the last snow fall, whereas in May 2012, only two days had elapsed. Despite this difference, May 2012 occupancy estimates were higher than those for April 2012, indicating that seasonal movement of ptarmigan into the study area occurred.

Seasonal colonization was greater at lower latitudes in 2011, consistent with our prediction that more southerly latitudes would be colonized early in the season, as ptarmigan moved north from southern wintering grounds. Contrary to expectations, colonization increased with increasing latitude in 2012, such that unoccupied survey units at northern latitudes were more likely to be colonized than their southern counterparts. This lends support to the idea that in the moderate snow year of 2012, ptarmigan migrated to Arctic breeding grounds and colonized unoccupied survey units in northern parts of the survey area earlier in the season than in 2011.

Within a season, the probability of occupancy by ptarmigan was higher if the survey unit was occupied the previous month. This is likely due to the continual use of high-quality shrub habitats by ptarmigan moving through the area. This indicates that a suitable habitat patch in March is likely to remain suitable in April and May and implies that ptarmigan do not exhaust

their food source after one visit. It is likely that spring snow melt exposes previously buried shrubs, providing a renewed food source for ptarmigan in areas they have already browsed. The Markovian dynamics were not as pronounced between years as they were within years; the probability of occupancy was not substantially greater in units that were occupied the previous year. The greater length of time between surveys may have caused this, where several Markovian changes occurred between years (Mackenzie et al. 2006). This may also be a result of high colonization rates in survey units containing shrubs in 2012, regardless of whether they were occupied in 2011. Under average shrub conditions, both occupied and unoccupied units in 2011 had a high (>90%) chance of being colonized the following year.

The discrepancy between occupancy of tracks versus ptarmigan themselves is helpful for understanding the ecology of this herbivore. Despite the fact that extensive shrub patches had a high probability of being visited by ptarmigan since the last snow fall (hence, distinguishable tracks), these patches had a much lower probability of actually hosting ptarmigan at any given time. Ptarmigan appeared to be highly mobile on the Arctic landscape, and were likely moving frequently to exploit patches with easily reachable buds. A preference for buds within easy reach was described by Tape et al. (2010), who found that the majority of browsing by ptarmigan occurred within 30 cm of snow level, with less browsing at greater heights. The decision to move to a new shrub patch once the easily accessible buds have been removed would presumably be a trade-off between maximizing food intake and minimizing energy expenditure (MacArthur and Pianka 1966). This will depend on the expected gain in current and alternative foraging areas and the distance to the next patch (Owen-Smith 2005).

Ptarmigan are ubiquitous in the river valleys of northern Alaska, where they congregate in flocks in the spring and fall. The reason for their abundance in the Arctic is linked to the quantity of high-quality habitat available to them. Large rivers with early successional floodplains dominated by tall willows provide vast amounts of habitat for ptarmigan in the winter and spring, and it appears, based on high probability of colonization of units with moderate shrub cover, that almost all suitable habitats within our study region were used by ptarmigan during this time. Climate change will continue to alter the Arctic landscape in many ways, some of which (shrub expansion) will increase habitat for ptarmigan. Observed differences between a high and moderate snow year indicate that ptarmigan occupancy is higher and migration may be earlier in years of greater habitat availability. Future shrub expansion may therefore benefit ptarmigan populations in the winter and spring. However, the dependence of ptarmigan on woody shrubs varies seasonally. Rock and willow ptarmigan specialize on birch and willow buds, respectively, in the winter, but become less specialized in the summer and fall, when adults consume tundra plants and their young consume insects (Hannon et al. 1998; Montgomerie and Holder 2008). How climate change will affect ptarmigan during the breeding season is unknown; if shrubs continue to invade tundra ecosystems, this could reduce the amount of tundra habitat for these species during the breeding season.

Our data show that areas with moderate to high shrub cover in northern Alaska have a high probability of being occupied by ptarmigan. By browsing the buds of willows and other woody shrubs in these areas, ptarmigan are likely to have a strong influence on plant growth and architecture, which in turn will affect plant community interactions, nutrient dynamics, and surface albedo. Ptarmigan therefore have the potential to interact strongly with shrub expansion,

a process that is well underway at northern latitudes (Chapin et al. 1995; Sturm et al. 2001; Walker et al. 2006; Tape et al. 2006). By removing the terminal buds from shrubs, ptarmigan essentially "prune" them, and this process is likely to be a pervasive force affecting the architecture and ecology of rapidly expanding shrubs in the Arctic (Hakkarainen et al. 2007; Tape et al. 2010).

2.6 Acknowledgements

This research was funded by a Natural Science and Engineering Council (NSERC) of Canada post-graduate scholarship to K.S.C., Alaska EPSCoR, and the University of Alaska Fairbanks Institute Of Arctic Biology. We thank Coyote Air Services for flying the surveys and facilitating the research. We would like to acknowledge Ken Tape for his help in the development of this project, Christa Mulder, Brett Sandercock, and anonymous reviewers for valuable comments on the manuscript, and Josh Schmidt for help with the analysis. Finally, we would like to thank field technicians Jeff Liechty, Aleya Nelson, Katie Rubin, Rick Merizon, Nat Nichols, and Neil Paprocki for assisting with aerial surveys. Use of trade names does not imply endorsement by the U.S. Government.

2.7 References

Andreev A (1988) The ten year cycle of the willow grouse of Lower Kolyma. Oecologia 76:261–267.

Bergerud A, Gratson M (1988) Survival and breeding strategies of grouse. In: Bergerud A, Gratson M (eds) Adapt. Strateg. Popul. Ecol. North. Grouse. University of Minnesota Press, Minneapolis, pp 473–577

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd Edition. Springer-Verlag, New York

Chapin FS, Shaver GR, Giblin AE, et al. (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Ehrich D, Henden J-A, Ims RA, et al. (2012) The importance of willow thickets for ptarmigan and hares in shrub tundra : the more the better? Oecologia 168:141–51. doi: 10.1007/s00442-011-2059-0

Gardarsson A, Moss R (1970) Selection of food by Icelandic ptarmigan in relation to its food availability and nutritive value.In: Watson A (ed) Animal populations in relation to their foodresources. Blackwell Scientific Publications, Oxford, pp 47–71

Gruys RC (1993) Autumn and winter movements and sexual segregation of Willow Ptarmigan. Arctic 46:228–239.

Hakkarainen H, Virtanen R, Honkanen JO, Roininen H (2007) Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biol 30:619–624. doi: 10.1007/s00300-006-0221-7

Hannon S, Eason P, Martin K (1998) Willow Ptarmigan (*Lagopus lagopus*). Birds North Am Online. doi: doi:10.2173/bna.369

Henden J-A, Ims RA, Yoccoz NG, Killengreen ST (2011) Declining willow ptarmigan populations: the role of habitat structure and community dynamics. Basic Appl Ecol 12:413–422. doi: 10.1016/j.baae.2011.05.006

Irving L, West C, Peyton LJ, Paneak S (1966) Migration of willow ptarmigan in arctic Alaska. Arctic 20:77–85.

Irving L, West GC, Peyton LJ (1967) Winter feeding program of Alaska willow ptarmigan shown by crop contents. Condor 69:69–77.

Jenkins D, Watson A, Miller G (1963) Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. J Anim Ecol 32:317–376.

Johnsgard P (1973) Willow Ptarmigan. Grouse Quails North Am. University of Nebraska Press, Lincoln, p 553

MacArthur R, Pianka E (1966) On the optimal use of a patchy environment. Am Nat 100:603–609.

Mackenzie D, Nichols J, Royle A, et al. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Waltham, Massachusetts

Montgomerie R, Holder K (2008) Rock Ptarmigan (*Lagopus muta*). Birds North Am Online. doi: doi:10.2173/bna.51

Moss R, Watson A (2001) Population cycles in birds of the grouse family. Adv Ecol Res 32:53–111.

Mossop DH (1988) Winter survival and breeding strategies of willow ptarmigan. In: Bergerud A, Gratson M (eds) Adapt. Strateg. Popul. Ecol. North. Grouse. Univerity of Minnesota Press, Minneapolis, pp 330–377

Myneni R, Keeling C, Tucker C, et al. (1997) Increased plant growth in the northern latitudes from 1981 to 1991. Nature 386:698–702.

Nichols JD, Hines JE, Sauer JR, et al. (2000) A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

Owen-Smith N (2005) Adaptive herbivore ecology: from resources to populations in variable environments, Second Edi. 392.

Schickhoff U, Walker MD, Walker DA (2002) Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. Phytocoenologia 32:145–204. doi: 10.1127/0340-269X/2002/0032-0145

Schwab FE, Simon NPP, Nash S (2005) Age and sex segregation of wintering willow ptarmigan in Labrador. Northeast Nat 12:113–118.

Sturm M, Racine C, Tape K, et al. (2001) Increasing shrub abundance in the Arctic. Nature 411:2001–2002.

Sturm M, Schimel J, Michaelson G, et al. (2005) Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55:17–26.

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob Chang Biol 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186–193. doi: 10.2980/17-2-3323

Walker MD, Wahren CH, Hollister RD, et al. (2006) Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci USA 103:1342–6. doi: 10.1073/pnas.0503198103

Weeden R (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

Weeden RB (1964) Spatial separation of sexes in Rock and Willow Ptarmigan in winter. Auk 81:534–541.

West G, Meng M (1966) Nutrition of willow ptarmigan in northern Alaska. Auk 83:603–615.

White G, Burnham K (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Williams JB, Best D, Warford C (1980) Foraging ecology of ptarmigan at Meade River, Alaska. Wilson Bull 92:341–351.

2.8 Figures

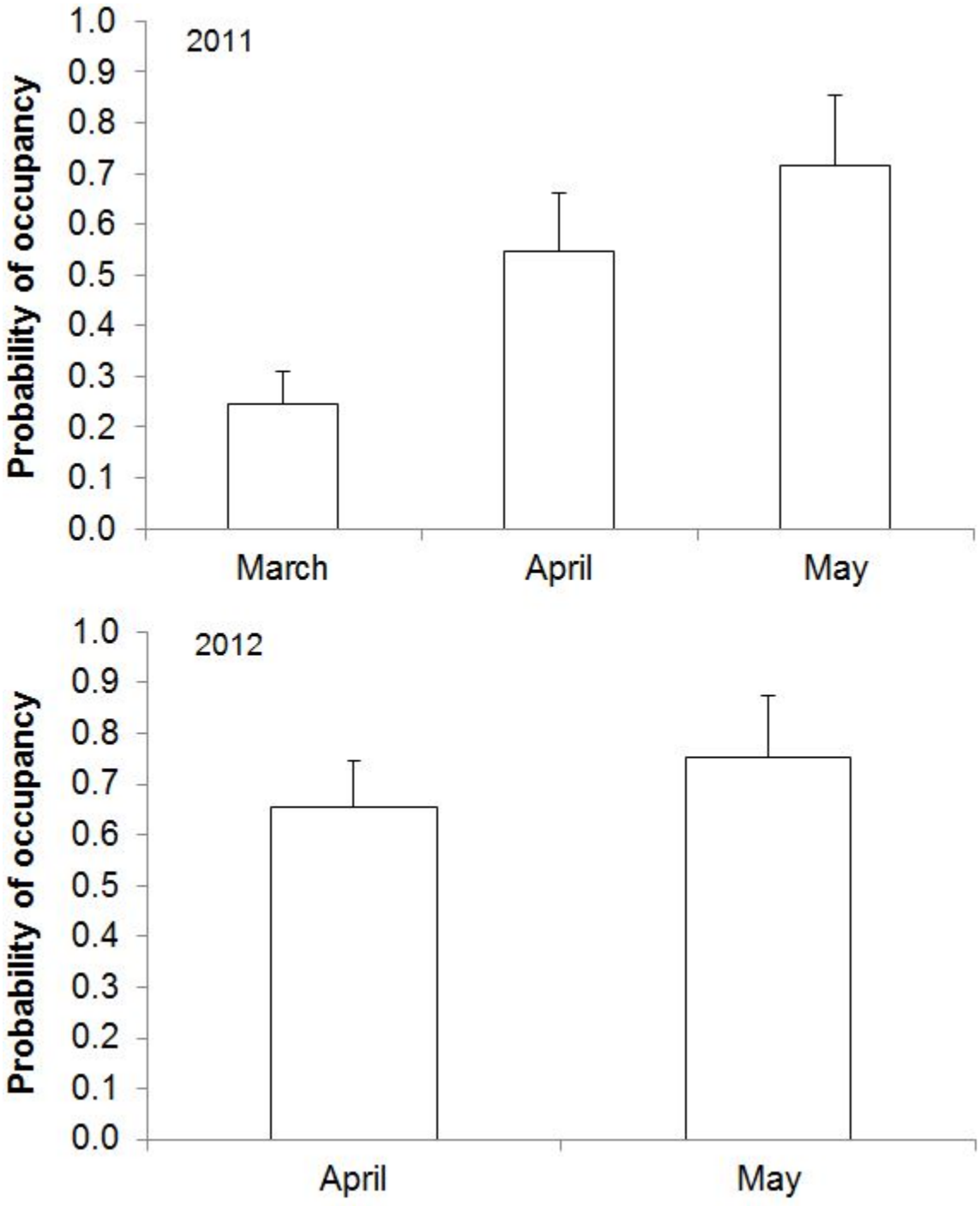

Figure 2-1. Probability of occupancy (± 95% CI) in March, April, and May 2011 and April and May 2012 at mean values of shrub cover and latitude

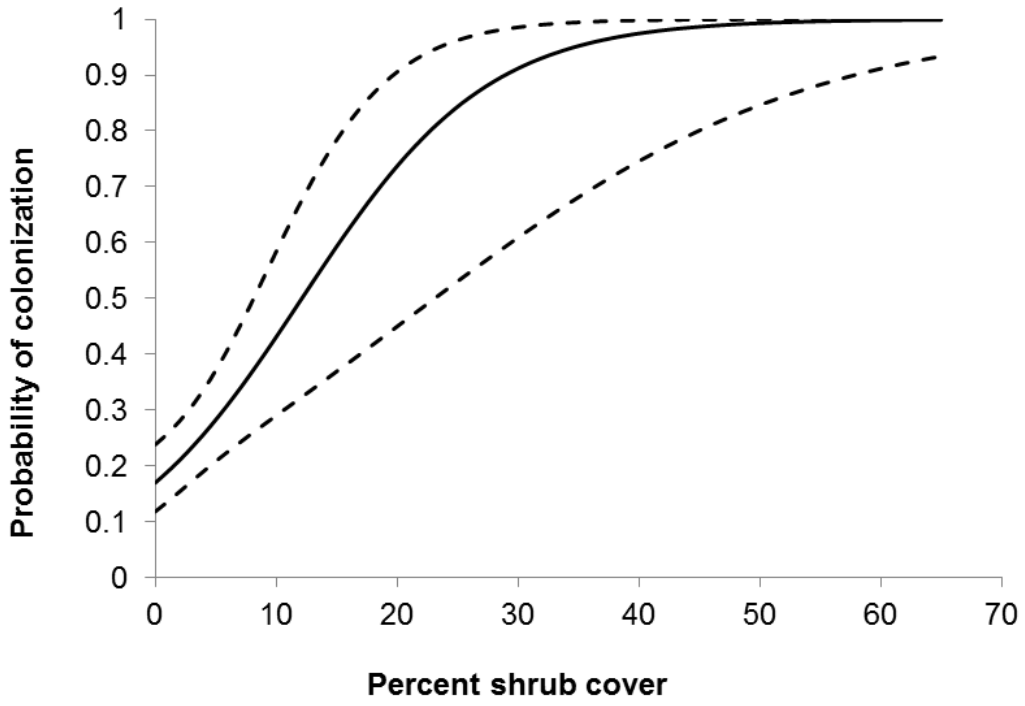

Figure 2-2. Relationship between probability of colonization from March to April to May 2011 and percent shrub cover. The solid line denotes colonization probability, and the dashed lines denote upper and lower confidence intervals

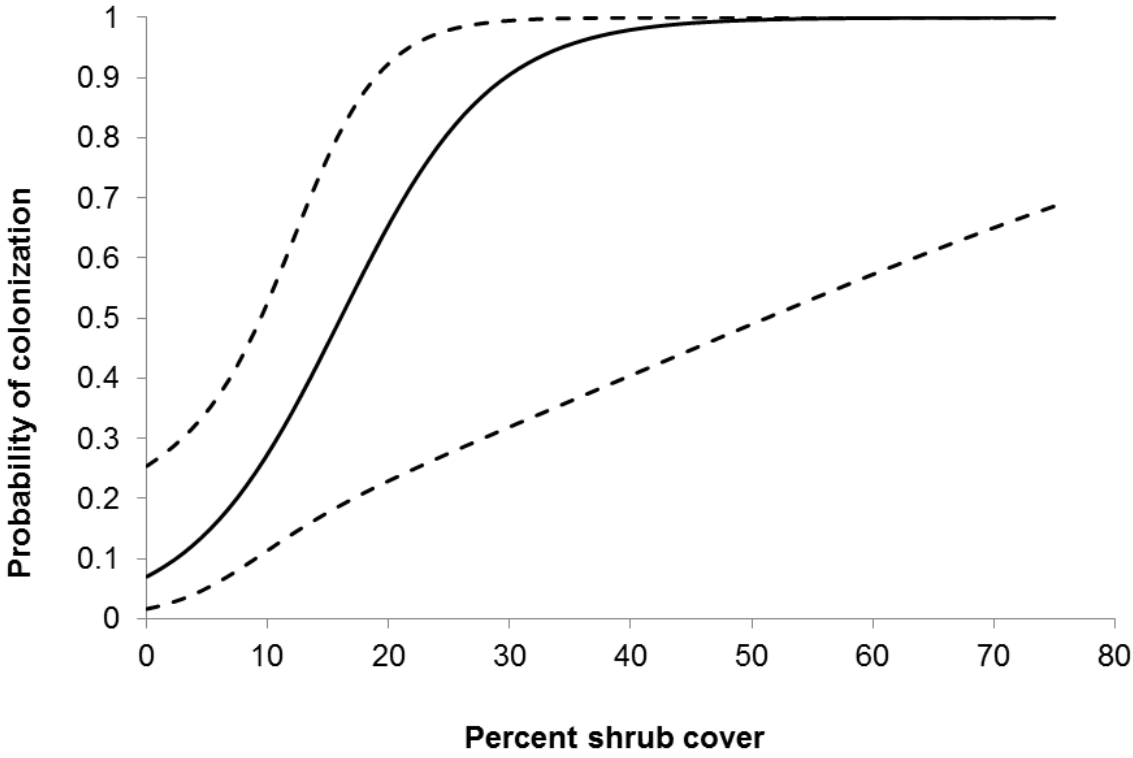

Figure 2-3. Relationship between probability of colonization from April to May 2012 and percent shrub cover. The solid line denotes colonization probability, and the dashed lines denote upper and lower confidence intervals

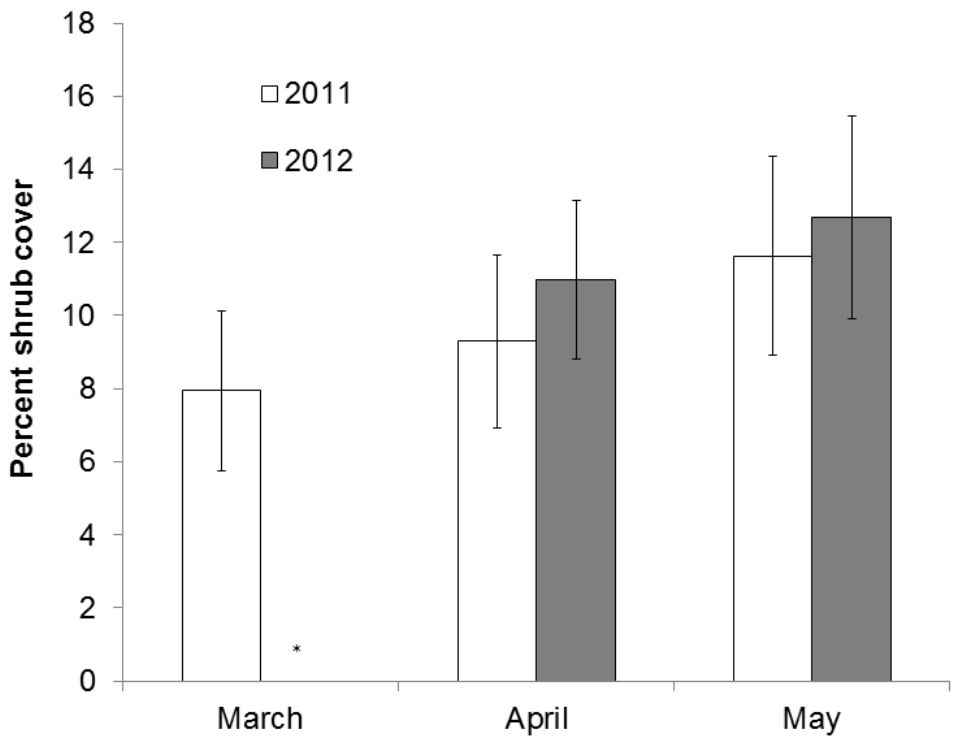

Figure 2-4. Average percent shrub cover (±95% confidence intervals) of survey units in March, April and May 2011 and April and May 2012. The asterisk denotes the fact that surveys were not conducted in March 2012

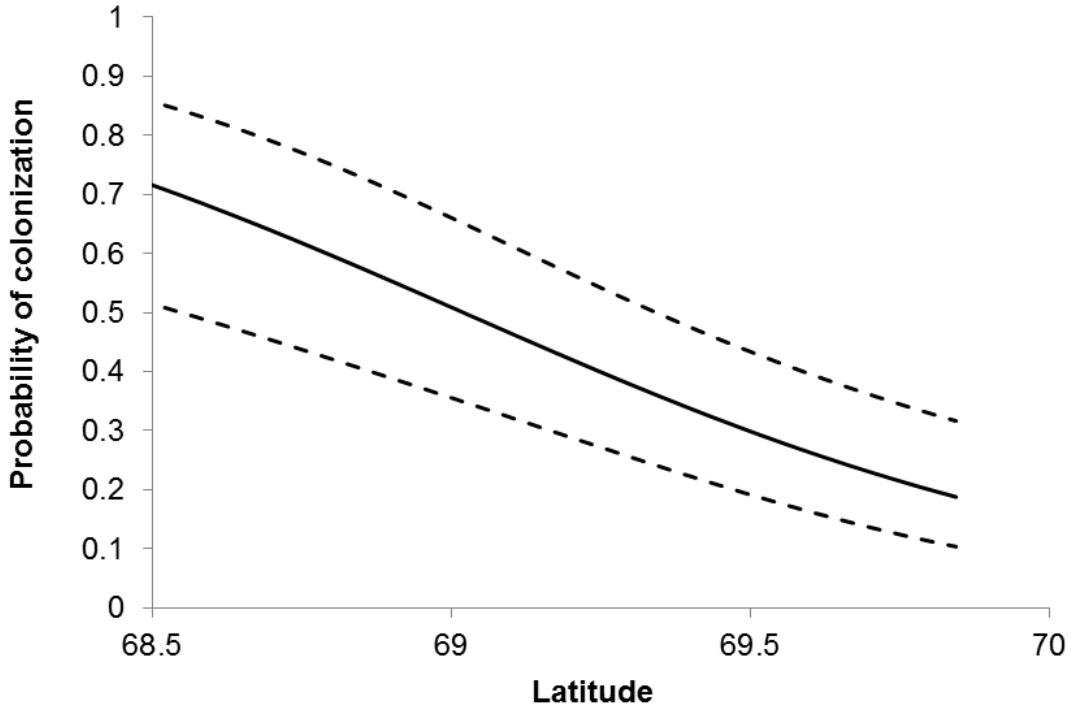

Figure 2-5. Relationship between probability of colonization from March to April to May 2011 and latitude. The solid line denotes colonization probability, and the dashed lines denote upper and lower 95% confidence intervals

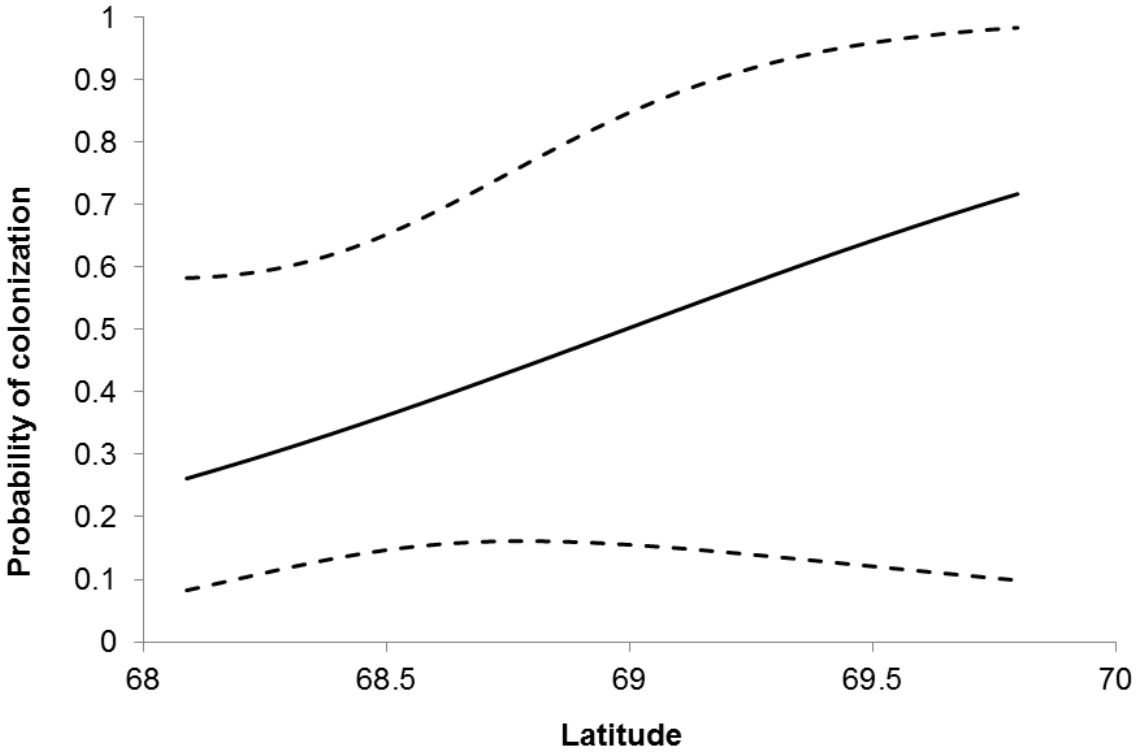

Figure 2-6. Relationship between probability of colonization from April to May 2012 and latitude. The solid line denotes colonization probability, and the dashed lines denote upper and lower 95% confidence intervals

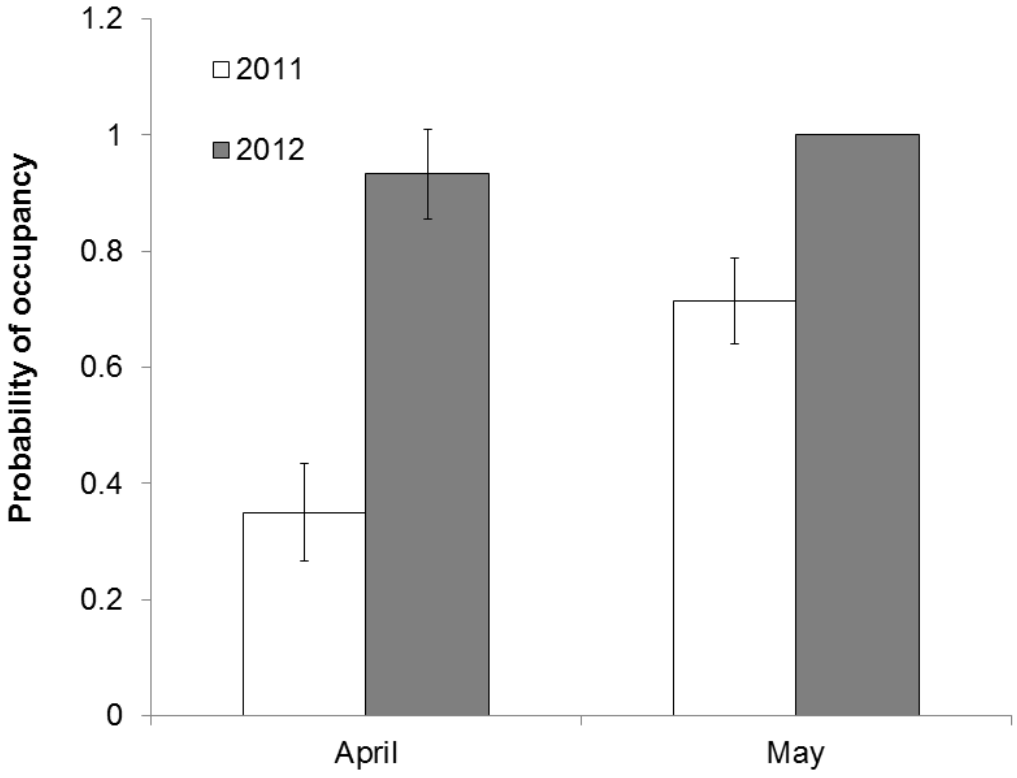

Figure 2-7. Estimates of probability of occupancy (±95% confidence intervals) in April and May 2011 and 2012 at mean levels of shrub cover. Estimates were obtained from two separate analyses comparing April 2011 to April 2012 and May 2011 to May 2012

2.9 Tables

Table 2-1. Models of occupancy (Ψ), colonization (γ), and extinction (ε) testing different hypotheses about ptarmigan population dynamics.

Model	Hypothesis
(Ψ.)γ(.)ε(.)	Colonization and extinction are constant
Ψ(.)γ(SC)ε(SC)	Colonization and extinction are dependent on percent shrub cover
Ψ(.)γ(ST)ε(ST)	Colonization and extinction are dependent on survey type (major river vs. random block)
Ψ(.)γ(Lat)ε(Lat)	Colonization and extinction are dependent on latitude
Ψ(.)γ(Lat+SC)ε(Lat+SC)	Colonization and extinction are dependent on latitude and shrub cover
Ψ(Mar = Apr = May)γ(.) OR Ψ(2011 = 2012)	No seasonal or annual change in occupancy
Ψ(.)γ(.)ε = 1-γ	Colonization and extinction rates do not depend upon previous occupancy state

Table 2-2. Model selection results for changes to ptarmigan occupancy from March to April to May 2011 and April to May 2012. Detection probability was modeled as a function of month in 2011 and was constant in 2012.

	2011				2012			
	ΔAICc	AICc Weights	Num Par	Deviance	ΔAICc	AICc Weights	Num Par	Deviance
Ψ(.)γ(Lat+SC)ε(Lat+SC)	0.00	1.00	10	804.35	0.00	1.00	8	472.56
Ψ(.)γ(SC)ε(SC)	17.94	0.00	8	826.44	26.62	0.00	6	503.45
Ψ(.)γ(Lat)ε(Lat)	26.96	0.00	8	835.46	34.91	0.00	6	511.74
Ψ(.)γ(ST)ε(ST)	29.26	0.00	8	841.88	36.01	0.00	6	514.95
Ψ(.)γ(.)ε(.)	45.23	0.00	5	859.90	42.00	0.00	4	523.02
Ψ(Mar=Apr=May)γ(.)	94.71	0.00	5	909.38	40.87	0.00	3	523.95
Ψ(.)γ(.)ε=1-γ	191.18	0.00	5	1005.85	73.94	0.00	3	557.03

Table 2-3. Parameter estimates of occupancy, extinction, colonization, and detection from the highest-ranked model of ptarmigan population change from March to April to May 2011 and April to May 2012. Month-specific detection probabilities are shown for 2011, but not 2012 because detection was modeled as a constant in 2012. Probability-scale estimates were calculated at mean values of shrub cover and latitude.

	2011				2012			
	Logit scale		Probability scale		Logit scale		Probability scale	
Parameter	estimate	SE	estimate	SE	estimate	SE	estimate	SE
Initial occupancy	-1.13	0.18	0.24	0.03	0.64	0.21	0.65	0.05
Extinction (intercept)	0.11	1.00	0.03	0.05	-6.03	2.11	0.05	0.04
Latitude (slope)	0.32	1.87	-	-	-13.79	4.87	-	-
Shrub cover (slope)	-0.39	0.23	-	-	-0.21	0.08	-	-
Colonisation (intercept)	-1.11	0.22	0.41	0.07	-2.11	0.77	0.37	0.14
Latitude (slope)	-1.78	0.39	-	-	1.15	1.08	-	-
Shrub cover (slope)	0.13	0.03	-	-	0.16	0.07	-	-

Table 2-3 (continued)

	2011				2012			
	Logit scale		Probability scale		Logit scale		Probability scale	
Parameter	estimate	SE	estimate	SE	estimate	SE	estimate	SE
p (March)	1.63	0.34	0.84	0.05	1.54*	0.18	0.82*	0.03
p (April)	1.03	0.25	0.73	0.05	-	-	-	-
p (May)	0.74	0.19	0.68	0.04	-	-	-	-

*The null model was used for p in 2012

Table 2-4. Model selection results for changes in ptarmigan occupancy from April 2011 to 2012 and from May 2011 to 2012. Detection probability was modeled as a function of observer in both analyses.

	April				May			
Model	ΔAICc	AICc Weights	Num Par	Deviance	ΔAICc	AICc Weights	Num Par	Deviance
Ψ(.)γ(SC+Lat)ε(SC+Lat)	0.00	0.54	9	459.64	0.00	0.99	9	669.38
Ψ(.)γ(SC)ε(SC)	0.30	0.46	7	464.20	9.30	0.01	7	682.90
Ψ(.)γ(ST)ε(ST)	54.99	0.00	7	518.90	34.67	0.00	7	708.27
Ψ(.)γ(.)ε(.)	58.54	0.00	5	526.65	36.66	0.00	5	714.42
Ψ(.)γ(Lat)ε(Lat)	62.07	0.00	7	525.97	28.65	0.00	7	702.25
Ψ(.)γ(.)ε=1-γ	81.82	0.00	4	552.01	104.05	0.00	4	783.88
Ψ(2011=2012)γ(.)	82.41	0.00	4	552.60	34.95	0.00	4	714.78

Table 2-5. Parameter estimates of occupancy, extinction, colonization, and detection from the highest-ranked model of ptarmigan population change from 2011 to 2012. Probability-scale estimates were calculated at mean values of shrub cover and latitude.

	April				May			
	Logit scale		Probability scale		Logit scale		Probability scale	
Parameter	estimate	SE	estimate	SE	estimate	SE	estimate	SE
Occupancy (2011)	-0.62	0.19	0.35	0.04	0.92	0.18	0.71	0.04
Extinction (intercept)	-0.52	1.06	0.13	0.09	-11.51	5.86	0.00	0.00
Latitude (slope)	1.18	1.84	-	-	-35.91	17.76	-	-
Shrub Cover (slope)	-0.14	0.11	-	-	-0.72	0.35	-	-
Colonization (intercept)	-3.54	0.97	0.97	0.04	-3.36	1.33	1.00	0.00
Latitude (slope)	1.68	0.96	-	-	-1.58	1.79	-	-
Shrub Cover (slope)	0.73	0.21	-	-	1.17	0.52	-	-
Observer 1	0.91	0.21	0.71	0.04	2.28	0.25	0.91	0.02
Observer 2	2.26	0.35	0.9	0.02	0.27	0.13	0.57	0.03

Chapter 3

Herbivores influence the growth, reproduction, and morphology of a widespread Arctic willow[2]

3.1 Abstract

Shrubs have expanded in Arctic ecosystems over the past century, resulting in significant changes to albedo, ecosystem function, and plant community composition. Willow and rock ptarmigan (*Lagopus lagopus, L. muta*) and moose (*Alces alces*) extensively browse Arctic shrubs, and may influence their architecture, growth, and reproduction. Furthermore, these herbivores may alter forage plants in such a way as to increase the quantity and accessibility of their own food source. We estimated the effect of winter browsing by ptarmigan and moose on an abundant, early-successional willow (*Salix alaxensis*) in northern Alaska by comparing browsed to unbrowsed branches. Ptarmigan browsed 82-89% of willows and removed 30-39% of buds, depending on study area and year. Moose browsed 17-44% of willows and browsed 39-55% of shoots. Browsing inhibited apical dominance and activated axillary and adventitious buds to produce new vegetative shoots. Ptarmigan- and moose-browsed willow branches produced twice the volume of shoot growth but significantly fewer catkins the following summer compared with unbrowsed willow branches. Shoots on browsed willows were larger and produced 40-60% more buds compared to unbrowsed shoots. This process of shoot production at basal parts of the branch is the mechanism by which willows develop a highly complex "broomed" architecture after several years of browsing. Broomed willows were shorter and more likely to be re-browsed by ptarmigan, but not moose. Ptarmigan likely benefit from the greater

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quantity and accessibility of buds on previously browsed willows and may increase the carrying capacity of their own habitat. Despite the observed tolerance of willows to browsing, their vertical growth and reproduction were strongly inhibited by moose and ptarmigan. Browsing by these herbivores therefore needs to be considered in future models of shrub expansion in the Arctic.

3.2 Introduction

Climate warming in the Arctic has resulted in the rapid expansion of woody shrubs over the past half-century (Chapin et al. 1995; Sturm et al. 2001; Walker et al. 2006; Tape et al. 2006). This shrub expansion has been likened to the melting of sea ice since shrubs (dark objects on the landscape) lower ground surface albedo, absorb heat, and accelerate snowmelt, thus creating a positive-feedback to climate warming (Sturm et al. 2005; Chapin et al. 2005). A process that will strongly interact with future climate warming to shape Arctic ecosystems is herbivory, which can significantly reduce the biomass of shrub species that would otherwise become dominant under warmer conditions (Gough et al. 2007; Post and Pedersen 2008; Olofsson et al. 2009). For example, a study of vegetation changes along a sub-Arctic river found that herbivory greatly reduced the proportion of willows on the landscape while increasing the proportion of thin-leaf alder (*Alnus tenuifolia* Betulaceae) (Butler et al. 2007).

Deciduous shrubs growing in productive areas have had the most pronounced and rapid response to climate change, but also experience the greatest levels of herbivory (Chapin et al. 1996; Sturm et al. 2001; Elmendorf et al. 2012) . Although the expansion of deciduous shrubs is known to be strongly regulated by herbivores (Gough et al. 2007; Ravolainen et al. 2011; Pajunen et al. 2012) this plant functional group has also shown remarkable resilience to herbivory (Henry and Gunn 1991; Yu et al. 2011). The degree to which deciduous shrubs are regulated by herbivores will depend on the frequency and intensity of herbivory, site productivity, and the tolerance of the forage species.

Herbivores are capable of altering the morphology, productivity, and chemistry of preferred species (McNaughton 1984; Danell et al. 1994), which in turn influence the population dynamics of both plants and herbivores (Fox and Bryant 1984; Person et al. 2003). In some

plant-herbivore systems, herbivory results in an increase in quality, quantity, and/or accessibility of food, and these areas are called "grazing lawns" (Hilbert et al. 1981; McNaughton 1984; Hik and Jefferies 1990; Du Toit et al. 1990). Mechanisms causing this phenomenon include fertilization via urine and feces and changes to plant physiology and development that facilitate compensatory growth (McNaughton 1983). These high-quality foraging areas, maintained by repeated grazing, have a greater carrying capacity and support more animals than un-grazed areas (Person et al. 2003). This process is not limited to grazing systems; browsers of woody plants can also increase the palatability, accessibility, and biomass of their food resources (Du Toit et al. 1990; Makhabu et al. 2006; Skarpe and Hester 2008). However, not all plant-herbivore systems lend themselves well to the creation of grazing lawns. Depending on the intensity of herbivory, plant physiological and genetic constraints, and water and nutrient availability, plants can increase, decrease, or have the same aboveground productivity relative to un-grazed plants. These responses represent over-compensation, under-compensation, and exact compensation, respectively (McNaughton 1983; Stewart et al. 2006).

In northern Alaska, moose (*Alces alces*) and ptarmigan (*Lagopus lagopus, L. muta*) concentrate in Arctic riparian areas where forage productivity is high and willows grow tall enough to exceed snow depth in winter (Figure 3-1). An important winter and spring food source for ptarmigan and moose in northern Alaska is feltleaf willow (*Salix alaxensis;* Salicaceae, Andersson), which is often the only willow species available for browsing in winter (Weeden 1969; Risenhoover 1989). Feltleaf willows establish on newly formed alluvial deposits, and their distribution is therefore tightly linked to fluvial dynamics of rivers. Over time and increasing distance from the riparian floodplain, feltleaf willows are replaced by later successional species such as Siberian alder (*Alnus viridis fruticosa*), dwarf birch (*Betula nana*; Betulaceae), and other

willows (e.g. *Salix lanata*, *Salix glauca*; (Schickhoff et al. 2002). High frequencies of browsing of willows in Arctic river valleys suggest that ptarmigan and moose may have a large cumulative impact on riparian shrub communities (Masters et al. 1980; Tape et al. 2010).

Many species of willows are remarkably tolerant to mammalian browsing, and respond by producing shoots with increased biomass and nutritional quality after being browsed (Fox and Bryant 1984; Molvar et al. 1993; Danell et al. 1994; Bryant 2003). These changes confer advantages to herbivores and can result in selectivity for previously browsed twigs (Bowyer and Neville 2003; Stolter 2008). However, the effects of browsing by avian herbivores such as ptarmigan are not well understood, and may or may not be similar to those of mammalian browsing. Ptarmigan are highly abundant herbivores and congregate in large aggregations to feed on woody shrubs in the Arctic (flocks of tens of thousands have been observed (Irving et al. 1966)), and it is therefore important to define their impact on Arctic shrub communities. Ptarmigan feed predominantly on willow buds that are closest to the surface of the snow (Hakkarainen et al. 2007; Tape et al. 2010), and typically remove the terminal buds, causing the shoot to die and new shoots to form from buds at the base of the branch (Tape et al. 2010). This results in a highly complex, "broom-like" , architecture (Tape et al. 2010). In addition to changes to architecture, browsing by ptarmigan may increase bud population growth rates, as observed by Tolvanen et al. (Tolvanen et al. 2002) in muskox (*Ovibos moschatus*) -grazed willows. Increased bud production, in combination with broomed architecture may be beneficial for future ptarmigan browsing because the two processes result in higher concentrations of buds within easy reach of ptarmigan.

This study addresses three important questions. 1) What is the extent and intensity of browsing on feltleaf willows? 2) What are the mechanisms by which ptarmigan and moose

influence the growth and reproduction of feltleaf willows? 3) Do ptarmigan and moose increase forage availability through browsing, thereby creating and maintaining "browsing hedges" in Arctic shrub ecosystems? We used stage-structured population models to quantify how the survival and production of new buds differ between browsed and unbrowsed willows, and how this in turn influences bud abundance, shoot and catkin production, and plant architecture.

3.3 Materials and Methods

Study area

We applied for and received permits to conduct our research on federal lands (NPS Permit# NOAT-2012-SCI-006; BLM Permit #FF095785). This study did not require the use of endangered or protected species. We selected two geographically distinct regions in northeastern and northwestern Alaska known to have ptarmigan and moose populations associated with willow thickets tall enough to exceed maximum snow depth. One study area was located along a 45 km segment of the upper Noatak River in the Noatak National Preserve (68.0°N,158.0°W to 68.0°N, 159.2°W), which flows westward from the Brooks Range in the Gates of the Arctic National Park to the Chukchi Sea. The other study area consisted of a 157 km stretch of the Dalton Highway, between Galbraith Lake and Franklin Bluffs (68.5°N, 149.5°W to 69.7°N, 148.7°W). Four of the five Dalton Highway sites were adjacent to the Sagavanirktok River, a major river flowing north from the Brooks Range to the Beaufort Sea. The southern-most site consisted of a gravel bar adjacent to Galbraith Lake. Other than this site, both study areas were located on wide, braided sections of the rivers, which flow through glacier-carved valleys surrounded by rolling hills. The plant communities in both study areas were characterized by a band of tall shrubs, dominated by feltleaf willow on floodplains, lower terraces, or gravel bars

adjacent to the river. Vegetation transitioned to shorter willows (e.g. *Salix lanata*, *Salix glauca*), dwarf birch, and Siberian alder further from the river's edge (Schickhoff et al. 2002).

Feltleaf willow transects

Twenty sites along the Noatak (10 sites) and Sagavanirktok Rivers (10 sites) were initially selected for sampling based on the presence of feltleaf willow stands. Of these, 5 sites from each study area were selected for the present study using systematic sampling with an initial random selection to determine whether the first or second of the 10 sites should be sampled, and alternating sites were sampled thereafter. Sites consisted of feltleaf willow stands varying in size from approximately 3 to 100 ha. At each of the 10 study sites, 30-40 feltleaf willow plants were randomly chosen, labeled, and marked with flagging tape in June 2011. We randomly chose feltleaf willows such that all ramets in the riparian zone had an equal probability of being sampled. When a willow was identified for sampling, a random branch was selected, marked, and assessed for browsing that occurred over the winter (2010-2011) and for type of browser (Figure 3-2). Occasionally, for very small willows, the entire ramet was measured. Herbivores could be identified by the browse marks left on the willow. Ptarmigan removed the buds and occasionally stripped the bark from willow shoots, whereas moose removed complete portions of shoots, leaving behind remnants measuring approximately 4-9 mm in diameter at the point of browse (Masters et al. 1980). Hares typically leave a sharp 45° angle on browsed shoots. We quantified the number of buds removed by ptarmigan by counting distinct orange bud scars left on the shoot after bud removal. The number of buds remaining on each shoot, number of shoots browsed by mammals, and shoots that remained (unbrowsed shoots) were also counted. These measures of browse were used to estimate intensity of browsing (proportion of buds or

shoots that had been removed). The entire branch, including remaining willow buds, catkins, shoots, and scars where buds had been removed was marked with color paint and mapped, so that the fate of buds and vegetative shoots could be determined the following spring (Figure 3-3).

Marked willow branches were re-visited and mapped in June 2012 to document browsing that occurred over the previous winter, and to record plant characteristics such as height, catkin production, shoot growth, and bud production (Figure 3-2). Surveys were conducted at the beginning of the growing season, and therefore measurements of shoot growth and bud production in 2012 represented the previous year's growth (2011 growing season). Annual shoot growth was quantified by measuring diameter and length of vegetative shoots produced the previous growing season (2011). It was possible to differentiate 2011 growth from current (2012) annual growth because the former was woody and brown and the latter light green. Marked willows were also measured for height, whether any shoot on the plant had been recently browsed by moose or ptarmigan (this was later used to calculate browsing frequency), and the percent of branches that were "broomed" (where >2 shoots originate from a single node on the branch). This is indicative of historic browsing intensity: a plant with many broomed branches had been subjected to several consecutive years of browsing by ptarmigan or moose (Danell et al. 1994; Tape et al. 2010).

Data analysis

Response of willow growth to herbivory

We quantified plant response to browsing based on the frequency and intensity of browsing by ptarmigan and moose at each site. Browsing intensity was measured as the proportion of shoots browsed by moose, and the proportion of buds removed by ptarmigan.

Occasional browsing by snowshoe hares (*Lepus americanus*) was identifiable by distinct browsing marks on willow shoots and these plants were discarded from the analysis.

We assessed the effects of ptarmigan and moose browsing on subsequent catkin production (2011) and shoot volume (2012; Figure 3-2). Mixed linear models were used to model fixed effects (browse status - "unbrowsed", "ptarmigan-browsed", or "moose-browsed") and random effects (site) using package "nlme" in program R (R Development Core Team version 2.15.1). Plants that were browsed by both ptarmigan and moose were classified as moose-browsed because usually only a few buds had been browsed by ptarmigan below the point of browse by moose and the effect of ptarmigan was in large part negated by moose. For shoot volume, we wished to examine the plant response to browsing that took place over the winter of 2010-2011, so we measured the mean volume of all shoots per random branch and total volume of shoots produced during the 2011 growing season. Shoot volume was calculated using the equation for a cone, using length and diameter at the base of the annual growth from 2011. Willows that were browsed by moose the subsequent winter (2011-2012) were not included in the analysis because new vegetative growth, including buds, had been consumed and could not be measured. Catkins were counted in the spring of 2011 to quantify direct removal of catkin-producing buds by both browsers during the winter of 2010-2011.

We tested whether a willow's past exposure to browsing was related to a) decreased plant height and b) increased likelihood of re-browsing. We assumed that highly broomed plants were exposed to intensive browsing for multiple years in the past. Tests for the existence of a negative relationship between proportion of branches broomed and height were conducted using linear mixed effect models with proportion of branches broomed as the fixed effect and site as the random effect. The probability of browsing by a moose or ptarmigan given the willow's historic

exposure to browsing was assessed using a mixed logistic regression, with a binary response variable (browsed/unbrowsed). The probability of browsing was modeled as a function of the proportion of branches that were broomed (fixed effect), and site (random effect). Data on brooming and browsing collected in spring 2012 were used for this analysis.

Bud demographic modeling

Bud demography models are a useful tool for understanding the effects of browsing on woody plants at the individual and population level (Tolvanen et al. 2002). Stage-based matrix population models (Caswell 2001) were used to compare bud population dynamics of ptarmigan-browsed and unbrowsed willows. See Text S1 for a detailed description of this analysis. It was not possible to conduct a bud demography study for moose-browsed willows because buds could not be counted after browsing. We predicted that willows would compensate for bud loss from browsing by stimulating dormant buds to produce vegetative shoots (themselves bearing buds) and increasing rates of bud production. For browsed and unbrowsed plants, we estimated mean vital rates for each stage in the bud life cycle and used these to calculate bud population growth rates. These demographic rates influence the production of vegetative shoots, plant architecture, bud abundance, and future food availability for ptarmigan.

3.4 Results

A total of 182 felt leaf willows in the Dalton and 190 willows in the Noatak study area were surveyed. Browsing by ptarmigan and moose were the most prevalent types of browsing observed in our study areas. Browsing by hares and rodents was occasionally observed, and winter browsing by muskox and caribou (*Rangifer tarandus*) was not observed. Ptarmigan

browsing occurred more frequently than moose browsing. In 2011, 88.5 ± 0.1% (SE) and 84.7 ± 0.1% of feltleaf willows were browsed by ptarmigan in the Dalton and Noatak study areas, respectively. Browsing frequencies by ptarmigan were similarly high in 2012, at 87.4 ± 0.1% in the Dalton and 81.6 ± 0.1% in the Noatak study area. In the Dalton study area, browsing by moose increased from 16.5 ± 0.1% of willows in 2011 to 36.8 ± 0.1% in 2012. In the Noatak study area, moose browsing frequency was similar between years at 44.2 ± 0.1% in 2011 and 42.6 ± 0.1% in 2012. In the Dalton study area, 15.9 ± 0.01% (2011) and 35.7 ± 0.01% (2012) of willows were browsed by both herbivores. At the Noatak study area, 37.9 ± 0.01% and 33.2 ± 0.01% of plants were browsed by both herbivores in 2011 and 2012, respectively. Hare browsing was low and inconsistent between years. In the Dalton study area, hares browsed no willows in 2011 and 8.8 ± 0.04% of willows in 2012, all of which occurred at a single site. In the Noatak study area, hares browsed 3.7 ± 0.02% of willows in 2011 and no willows in 2012. The majority of willows survived for the duration of the study; only three out of 372 willows died. Of the branches examined for browsing, ten died between 2011 and 2012 surveys, three of which were browsed by hares. The remaining seven branches were unbrowsed and died of unknown causes. The distal portions of shoots that had been browsed by ptarmigan usually died.

Ptarmigan and moose browsing intensity remained fairly consistent across years and sites; ptarmigan typically removed over a third of buds on willow branches, and moose browsed almost half of all new shoots. Ptarmigan removed a mean of 37.1 ± 2.4% (SE; Dalton) and 36.1 ± 2.1% (Noatak) of buds in 2011 and 38.9 ± 2.4% (Dalton) and 30.3 ± 2.2% (Noatak) of buds in 2012. Bud removal by ptarmigan was focused on the terminal end of shoots grown the previous growing season, and a few buds often remained at the base of each browsed shoot. In 2011, moose browsed a mean of 45.0 ± 4.5% of shoots per branch in the Dalton study area and 55.4 ±

3.8% of shoots per branch at the Noatak. Browsing intensity was slightly lower in 2012; moose browsed 39.0 ± 4.4% of shoots at the Dalton and 45.5 ± 4.2% of shoots at the Noatak study area.

Ptarmigan and moose-browsed willow branches produced shoots that were approximately twice (178 – 261%) as large in volume as unbrowsed willows (Figure 3-4a, moose: z-value = 2.1, $p = 0.03$, n=164, ptarmigan: z-value = 2.6, $p < 0.01$, n = 164). Browsed willow branches produced shoots that were longer and wider in diameter than shoots of unbrowsed branches. Total shoot volume (the sum of all individual shoots on a branch) was also significantly greater in browsed than unbrowsed branches for both herbivores (Figure 3-1b, moose: z-value = 6.1, $p < 0.001$, n = 164, ptarmigan: z-value = 3.7, $p < 0.001$).

Both herbivores strongly influenced catkin production by directly removing catkin-producing buds prior to the spring reproductive period. Ptarmigan-browsed willows had 25-50% fewer catkins (depending on the study area) and moose-browsed willow branches had 54-59% fewer catkins than unbrowsed willow branches (moose: z-value = -4.9, $p < 0.001$, ptarmigan: z-value = -5.5, $p < 0.001$, n = 372, Figure 3-5). Willows in the Noatak study area produced substantially fewer catkins than those in the Dalton study area.

By activating axillary (at the base of the shoot) and dormant adventitious (embedded in the cambium of older parts of the plant) buds for vegetative shoot production and increasing the number of buds per shoot, ptarmigan-browsed willows maintained similar population growth rates (λ: the change in number of buds per branch over time) to their unbrowsed counterparts (Dalton: $\lambda_{unbrowsed} = 1.49$, $\lambda_{browsed} = 1.37$; Noatak: $\lambda_{unbrowsed} = 1.35$, $\lambda_{browsed} = 1.35$). The LTRE (Life-table response experiment) analysis indicated that the largest contributor to variation in λ was the recruitment of new buds from dormant buds via the production of vegetative shoots (Dalton: 39% of total variation, Noatak: 51% of total variation; “F2”, Figure 3-6). Unbrowsed

and ptarmigan-browsed willows had different bud fecundities and transition probabilities for both new and dormant buds (Figure 3-7). The probability of a bud producing a vegetative shoot was 41-77% higher for unbrowsed willows than ptarmigan-browsed willows in both study areas, and this is likely a direct result of bud removal by ptarmigan, i.e., browsed willows had fewer buds available for vegetative shoot production ($\beta = -0.16$, t-value = -5.4, $p < 0.001$, $n = 125$, Figure 3-7a). However, browsed willows produced 40-60% more new buds per vegetative shoot than unbrowsed willows ($\beta = 1.29$, t-value = 3.3, $p = 0.001$, $n = 125$, Figure 3-7b). Fewer buds became dormant in browsed versus unbrowsed willows ($\beta = -0.17$, t-value = -5.0, $p < 0.001$, $n = 125$, Figure 3-7c). Dormant buds sprouted into vegetative shoots at higher rates in browsed versus unbrowsed willows at the Dalton study area but not at the Noatak, and the overall effect was not significant ($\beta = 0.07$, t-value = 1.22, $p = 0.23$, $n = 125$, Figure 3-7d). At the Noatak, none of the vegetative sprouts that originated from dormant buds on unbrowsed willows survived to produce bud-bearing shoots (Figure 3-7e). New vegetative shoots produced from dormant buds bore more buds on browsed plants than unbrowsed plants ($\beta = 0.97$, t-value = 2.10, $p = 0.04$, $n = 125$). Lastly, dormant buds stayed dormant at higher rates in unbrowsed versus browsed plants ($\beta = 0.48$, t-value = -2.06, $p = 0.04$, $n = 125$, Figure 3-7f).

Historic browsing, indicated by the proportion of broomed branches on the plant, was negatively related to total plant height ($\beta = -0.46 \pm 0.13$, t-value = -3.39, $p < 0.001$, $n = 356$) such that a heavily-broomed willow's height was reduced by 20% compared to an un-broomed willow (Figure 3-8, 3-9a). The probability of being browsed by ptarmigan increased significantly with the proportion of branches that were broomed (Figure 3-8b; z-value = 5.5, $p < 0.001$, $n = 348$), whereas no such relationship existed for moose (z-value = 0.88, $p = 0.38$, $n = 348$).

3.5 Discussion

Ptarmigan and moose strongly influenced willow biology in two geographically disparate regions of northern Alaska. Feltleaf willows responded to browsing by activating axillary and adventitious buds, and by producing long shoots with many buds. Repeated browsing resulted in short, structurally complex plants. Ptarmigan (but not moose) appeared to feed more frequently on these willows, which produced a food resource (buds) that was both accessible and concentrated. Early successional feltleaf willow stands provide optimal habitat for ptarmigan and moose not only because they grow tall enough to exceed snow depth in winter, but also because they are highly tolerant of herbivory (Fox and Bryant 1984; Bryant 2003).

Willows that were browsed by ptarmigan or moose produced more than twice the volume of annual shoots compared with unbrowsed willows, indicating that feltleaf willows over-compensated for herbivory. Moderate herbivory can result in exact or over-compensation when plants have adequate access to nutrients and water and are inherently fast growing (Hilbert et al. 1981; Coley et al. 1985; Harrison and Bardgett 2008). Feltleaf willows adhere to these characteristics and have been known to compensate for moderate levels of herbivory by snowshoe hares (Fox and Bryant 1984; Bryant 2003). The production of large shoots after browsing is adaptive because it allows the plant to a) quickly grow to escape herbivory; b) produce vegetative shoots and leaves for photosynthesis; and c) increase bud production to replace buds lost to browsing. Willows appear to respond similarly to ptarmigan and moose browsing, because both browsers remove terminal and distal axillary buds and cause shoot die-off and shoot loss, respectively.

By removing distal axillary buds that would otherwise become catkins, ptarmigan and moose interfere with sexual reproduction. This in turn is likely to hinder the ability of feltleaf

willows to colonize areas such as newly formed alluvial surfaces, and may make them less competitive with other plants. Pollen and seed viability of Siberian alder, dwarf birch, and willows (*Salix* spp.) is expected to increase in the future as temperatures rise (Myers-Smith et al. 2011). However, for highly palatable willows, the consumption of catkins by herbivores will likely reduce their ability to compete with other, less-preferred species.

Ptarmigan-browsed and unbrowsed willows had similar bud population growth rates, but these were maintained through different pathways. An unbrowsed willow branch will gradually elongate as terminal and distal axillary buds develop into shoot primordia during the growing season (Archer and Tieszen 1980). Leaves are distributed evenly along shoots and new buds develop adjacent to leaf petioles at the end of the growing season. By removing terminal and distal axillary buds, ptarmigan stimulate willows to activate proximal axillary and dormant adventitious buds to produce tissue required for photosynthesis and future bud production. This activation of axillary and adventitious buds, combined with the increased numbers of buds produced per vegetative shoot, allows willows to maintain bud populations at similar levels to unbrowsed plants. Although we were unable to directly measure the effect of moose browsing on bud demographic rates, we suspect that a similar process occurs due to the removal of shoots bearing terminal and distal axillary buds, as observed in other studies of mammalian browsing (Archer and Tieszen 1980; Tolvanen et al. 2002).

The repeated removal of terminal buds by ptarmigan creates a broomed structure and constrains branch elongation, ultimately reducing the height of the willow, similar to how reindeer reduce the height of willows in Finnish Lapland and Siberia (den Herder et al. 2008; Olofsson et al. 2009; Pajunen 2009). A key consequence of the altered architecture of browsed willows, combined with greater numbers of buds per shoot, is an increase in food availability for

ptarmigan. Short, broomed willows are more accessible to ptarmigan, which prefer to feed on buds close to the snow (Hakkarainen et al. 2007; Tape et al. 2010). After several years of ptarmigan browsing, willows become "hedged" just above average snow level, providing optimal food accessibility for ptarmigan in future average snow years (Tape et al. 2010). By increasing the quantity and accessibility of available forage in future years, flocks of ptarmigan may be creating "browsing hedges" analogous to grazing lawns maintained by ungulates (McNaughton 1984; Stewart et al. 2006), sea turtles (Bjorndal 1980) and geese (Hik and Jefferies 1990; Person et al. 2003). In years of higher than average snow fall, willows may become buried and protected from browsing, whereas in years of lower than average snowfall, more willow branches become available for browsing. Food availability for ptarmigan is therefore strongly related to snow conditions of a given year. Whether these willows confer a nutritional advantage to ptarmigan in the form of increased quality of buds (McNaughton 1984; Du Toit et al. 1990) is beyond the scope of this paper and worthy of further investigation.

The greater volume of tissue produced by moose-browsed willow branches suggests that moose are also capable of increasing the quantity of their own food source. The compensatory response that we observed in feltleaf willows is consistent with observations of this species' response to mammalian browsing in boreal ecosystems (Bryant 1987; Bowyer and Neville 2003). Moose, however, did not show a preference for previously browsed (broomed) willows. In our study, broomed willows had been exposed to a combination of ptarmigan and moose browsing in the past. The architectural complexity of highly broomed willows, which consisted of clusters of both live and dead (ptarmigan-browsed) shoots, may have restricted access to live shoots by moose (Masters et al. 1980). Moose show a preference for woody plants with fewer, larger shoots, allowing for higher harvest rates (Niemela and Danell 1988; Shipley et al. 1998),

and discriminate against well-defended shoots (Stolter 2008; Rea 2012). Thus, by altering the architecture of willows, ptarmigan may reduce forage accessibility to moose. It is also possible that moose are deterred by secondary metabolites produced in the shoots of heavily broomed willows; feltleaf willows are known to produce less palatable twigs in response to severe browsing by snowshoe hares (Bryant et al. 1985).

Due to the observational nature of this study, it is necessary to consider alternative explanations for the observed differences between browsed and unbrowsed willows. For example, ptarmigan and moose may have chosen to browse willows with greater access to resources and/or inherently faster growth rates than unbrowsed willows. Furthermore, the architecture of willows could potentially be influenced by winter abrasion and desiccation [50]. However, if this were the case with feltleaf willows, we would expect to see dead or broken branches with no signs of browsing, which we did not. We expect that severe winter conditions may be more important in limiting the growth of shrubs that occur on exposed ridgetops than those growing in protected river valleys (Pajunen 2009). Nevertheless, a simulated browsing experiment would help to tease apart the effects of browsing from other potentially confounding factors on willow growth and architecture.

In this study, we examined the growth and bud production at the branch-level rather than the entire plant. This was necessary for efficiency of data collection and also because few willows in our survey area were completely unbrowsed. Some of the unbrowsed willow branches were therefore attached to willows that had experienced low-level browsing. The fact that we observed such strong differences between the two branch types reflects the tendency of branches to operate as separate modular units within the plant, with correspondingly distinct physical and chemical characteristics (Stolter 2008).

A large proportion of feltleaf willows in our study areas were browsed by ptarmigan, and browsing by this herbivore was at least three times more prevalent than browsing by moose. Ptarmigan browsed much higher proportions of buds in our study areas (30-40%) than in Finland, where only 6% of willow buds were browsed despite the fact that ptarmigan were at the peak of their cycle (Hakkarainen et al. 2007). The high frequency and intensity of browsing observed at our study sites reflect the importance of considering the effects of browsing by this small avian herbivore on Arctic shrub ecosystems in Alaska and perhaps elsewhere in North America. Surveys of spring ptarmigan distribution in northern Alaska indicated that shrub patches associated with small and large river drainages and areas with snow-free ground had a high probability (>85%) of being occupied by ptarmigan (Christie et al. 2014). The degree to which ptarmigan populations in the study area fluctuate is unknown, although surveys by Irving et al (Irving et al. 1966) over the course of 15 years suggest that they do not cycle in northern Alaska, as they do in other parts of their range. Moose generally occur in low densities in northern Alaska, and concentrate in large river drainages with tall shrubs that exceed snow depth (Mauer 1998). Although fewer willows were browsed by moose than by ptarmigan in our study areas, moose removed large amounts of tissue (45-55% of shoots per branch) and therefore also need to be considered as important Arctic herbivores.

Feltleaf willows were highly tolerant of herbivory and produced twice the volume of current annual growth relative to unbrowsed willows. This species of willow is in an optimal position to compensate for herbivory due to its inherently fast growth rate and tendency to grow on river floodplains, where frequent flooding provides access to water and nutrients. Despite its ability to tolerate browsing, the feltleaf willow experienced severely reduced reproductive output, and over the long term, distinctly altered height and architecture. By “pruning” willows

on an annual basis, ptarmigan and moose prevent them from reaching their full reproductive and physical potential. This in turn increases the susceptibility of willows to further attack, thereby benefitting ptarmigan populations. Although deciduous shrubs are known to be highly resilient to herbivory (Henry and Gunn 1991; Yu et al. 2011), repeated pruning by herbivores is likely to curtail their expansion in the Arctic and may facilitate the spread of less palatable species.

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We would like to thank Christine Hunter and Ken Tape for providing valuable advice in the early stages of this research. We thank Dirk Nickisch with Coyote Air for transport to study sites, and Karl Bachmann, Rebecca Hewitt, Johanna Hiscock, Catherine Minshull, Neil Paprocki, and Katie Rubin for their help in the field. We thank Brad Shults and Jim Lawler for logistic support, and Joel Schmutz, Sophie Gilbert, and anonymous reviewers for editing this manuscript.

3.7 References

Archer S, Tieszen LL (1980) Growth and physiological responses of tundra plants to defoliation. Arct Alp Res 12:531–552.

Bjorndal KA (1980) Nutrition and Grazing Behavior of the Green Turtle. Mar Biol 56:147–154.

Bowyer RT, Neville JA (2003) Effects of browsing history by Alaskan moose on regrowth and quality of feltleaf willow. Alces 39:193–202.

Bryant JP (1987) Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology 68:1319–1327.

Bryant JP (2003) Winter browsing on Alaska feltleaf willow twigs improves leaf nutritional value for snowshoe hares in summer. Oikos 1:25–32.

Bryant JP, Wieland GD, Clausen T, Kuropat P (1985) Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology 66:1564–1573.

Butler LG, Kielland K, Rupp TS, Hanley T (2007) Interactive controls of herbivory and fluvial dynamics on landscape vegetation patterns on the Tanana River floodplain, interior Alaska. J Biogeogr 34:1622–1631. doi: 10.1111/j.1365-2699.2007.01713.x

Caswell H (2001) Matrix Population Models, 2nd ed. Sinauer Associates Inc., Sunderland

Chapin FS, Bret-Harte SM, Hobbie SE (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. J Veg Sci 7:347–358. doi: 10.2307/3236278

Chapin FS, Shaver GR, Giblin AE, et al. (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Chapin FS, Sturm M, Serreze MC, et al. (2005) Role of land-surface changes in arctic summer warming. Science 310:657–60. doi: 10.1126/science.1117368

Christie KS, Lindberg MS, Ruess RW, Schmutz JA (2014) Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. Polar Biol. doi: 10.1007/s00300-014-1504-z

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899.

Danell K, Bergström R, Edenius L (1994) Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. J Mammal 75:833–844.

Elmendorf SC, Henry GHR, Hollister RD, et al. (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15:164–75. doi: 10.1111/j.1461-0248.2011.01716.x

Fox JF, Bryant JP (1984) Instability of the snowshoe hare and woody plant interaction. Oecologia 63:128–135.

Gough L, Ramsey EA, Johnson DR (2007) Rapid , landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Oikos 116:407–418. doi: 10.1111/j.2007.0030-1299.15449.x

Hakkarainen H, Virtanen R, Honkanen JO, Roininen H (2007) Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biol 30:619–624. doi: 10.1007/s00300-006-0221-7

Harrison KA, Bardgett RD (2008) Impacts of grazing and browsing by larger herbivores on soils and soil biological properties. In: Gordon IJ, Prins HHT (eds) The Ecology of Browsing and Grazing. Springer-Verlag, Berlin pp. 201-216.

Henry GHR, Gunn A (1991) Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic 44:38–42.

den Herder M, Virtanen R, Roininen H (2008) Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic Appl Ecol 9:324–331. doi: 10.1016/j.baae.2007.03.005

Hik ADS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: A test of the predictions of the herbivore-optimization model. J Ecol 78:180–195.

Hilbert ADW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Irving L, West C, Peyton LJ, Paneak S (1966) Migration of willow ptarmigan in arctic Alaska. Arctic 20:77–85.

Makhabu SW, Skarpe C, Hytteborn H (2006) Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. Acta Oecologica 30:136–146. doi: 10.1016/j.actao.2006.02.005

Masters M, Densmore R, Neiland B, Zasada J (1980) Moose utilization of riparian willow in the central Alaska North Slope. 16.

Mauer FJ (1998) Moose migration: Northeastern Alaska to Northwestern Yukon Territory, Canada. Alces 34:75–81.

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886.

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

Molvar EM, Bowyer RT, Van Ballenberghe V, Van Brauenberone V (1993) Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479.

Myers-Smith IH, Forbes BC, Wilmking M, et al. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:610–623. doi: 10.1088/1748-9326/6/4/045509

Niemela AP, Danell K (1988) Comparison of moose browsing on Scots pine (*Pinus silvestris*) and lodgepole pine (*P. contorta*). J Appl Ecol 25:761–775.

Olofsson J, Oksanen L, Callaghan T, et al. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. Glob Chang Biol 15:2681–2693. doi: 10.1111/j.1365-2486.2009.01935.x

Pajunen A, Virtanen R, Roininen H (2012) Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. Oikos 121:1544–1552. doi: 10.1111/j.1600-0706.2011.20115.x

Pajunen AM (2009) Environmental and biotic determinants of growth and height of Arctic willow shrubs along a latitudinal gradient. Arctic, Antarct Alp Res 41:478–485. doi: 10.1657/1938-4246-41.4.478

Person BT, Herzog MP, Ruess RW, Sedinger JS (2003) Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592. doi: 10.1007/s00442-003-1

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci USA 105:12353–12358. doi: 10.1073/pnas.0802421105

Ravolainen VT, Bråthen KA, Ims RA, et al. (2011) Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Basic Appl Ecol 12:643–653. doi: 10.1016/j.baae.2011.09.009

Rea R (2012) The influence of willow *Salix* sp. rose insect galls on moose *Alces alces* winter browsing. Can Field-Naturalist 126:189–193.

Risenhoover KL (1989) Composition and quality of moose winter diets in interior Alaska. J Wildl Manage 53:568–577.

Schickhoff U, Walker MD, Walker DA (2002) Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. Phytocoenologia 32:145–204. doi: 10.1127/0340-269X/2002/0032-0145

Shipley LA, Blomquist S, Danell K (1998) Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. Can J Zool 76:1722–1733.

Skarpe C, Hester A (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: Gordon IJ, Prins HHT (eds) The Ecology of Browsing and Grazing. Springer-Verlag, Berlin pp. 217-261.

Stewart KM, Bowyer RT, Ruess RW, et al. (2006) Herbivore optimization by North American Elk: consequences for theory and management. Wildl Monogr 167:1–24.

Stolter C (2008) Intra-individucal plant response to moose browsing: feedback loops and impacts on multiple consumers. Ecol Monogr 78:167–183.

Sturm M, Racine C, Tape K, et al. (2001) Increasing shrub abundance in the Arctic. Nature 411:2001–2002.

Sturm M, Schimel J, Michaelson G, et al. (2005) Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55:17–26.

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob Chang Biol 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186–193. doi: 10.2980/17-2-3323

Du Toit JT, Bryant JP, Frisby K (1990) Regrowth and Palatability of Acacia Shoots Following Pruning by African Savanna Browsers. Ecology 71:149–154.

Tolvanen A, Schroderus J, Henry GHR (2002) Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. Evol Ecol 443–462.

Walker MD, Wahren CH, Hollister RD, et al. (2006) Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci USA 103:1342–6. doi: 10.1073/pnas.0503198103

Weeden R (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

Yu Q, Epstein HE, Walker D, et al. (2011) Modeling dynamics of tundra plant communities on the Yamal Peninsula, Russia, in response to climate change and grazing pressure. Environ Res Lett 6:045505. doi: 10.1088/1748-9326/6/4/045505

3.8 Figures

Figure 3-1.Willow ptarmigan (*Lagopus lagopus*) near a felt-leaf willow (*Salix alaxensis*) stand in northeastern Alaska.

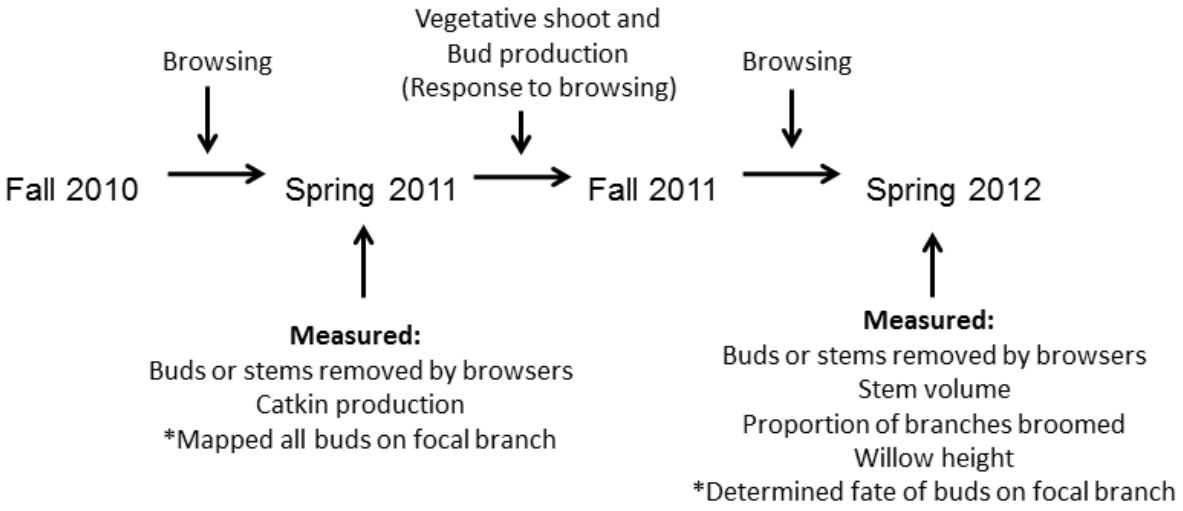

Figure 3-2. Timing of browsing and feltleaf willow (*Salix alaxensis*) growth in relation to timing of measurements.

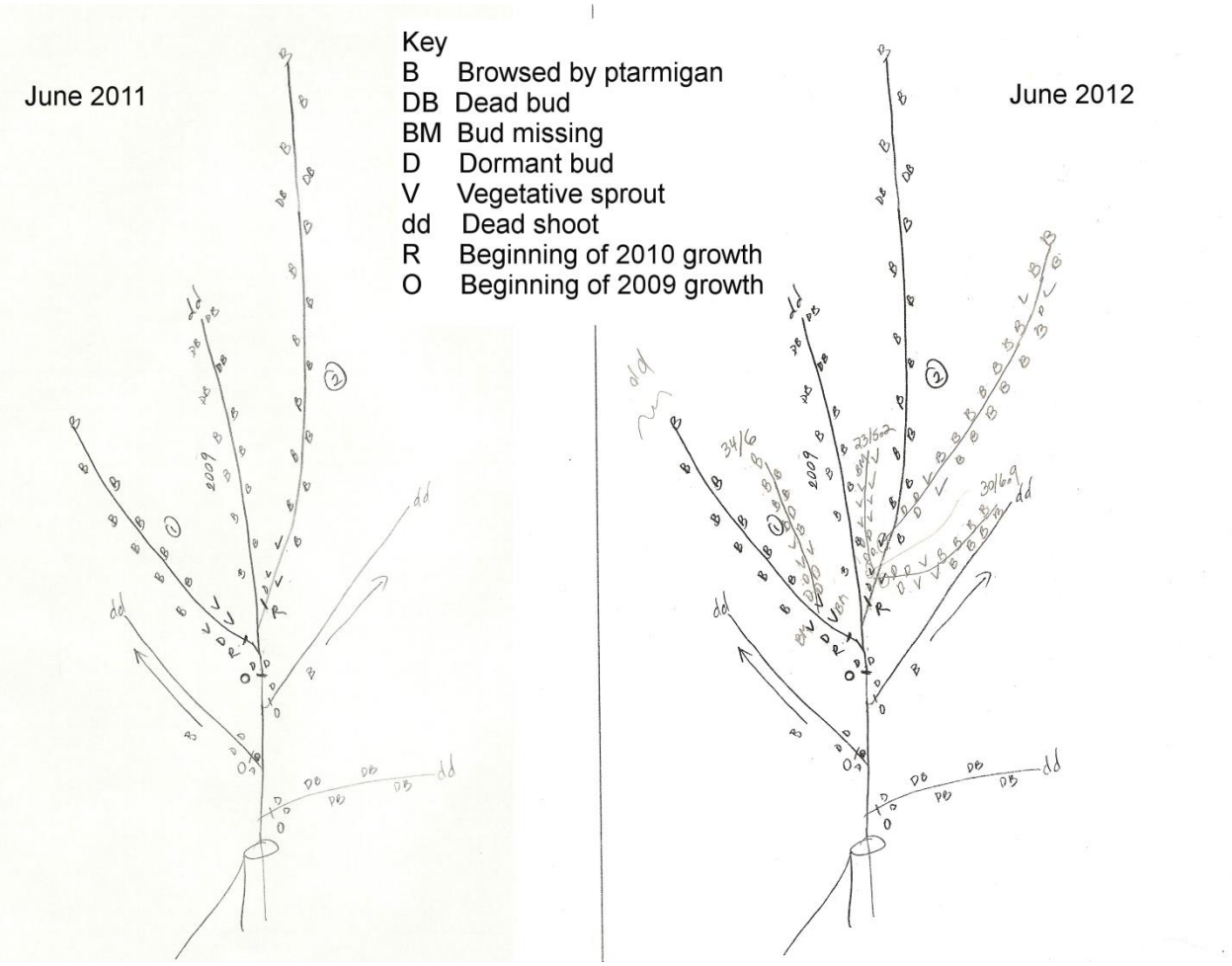

Figure 3-3. Map of felt-leaf willow branch first visited in June 2011 (left) and subsequently re-mapped in June 2012 (right).

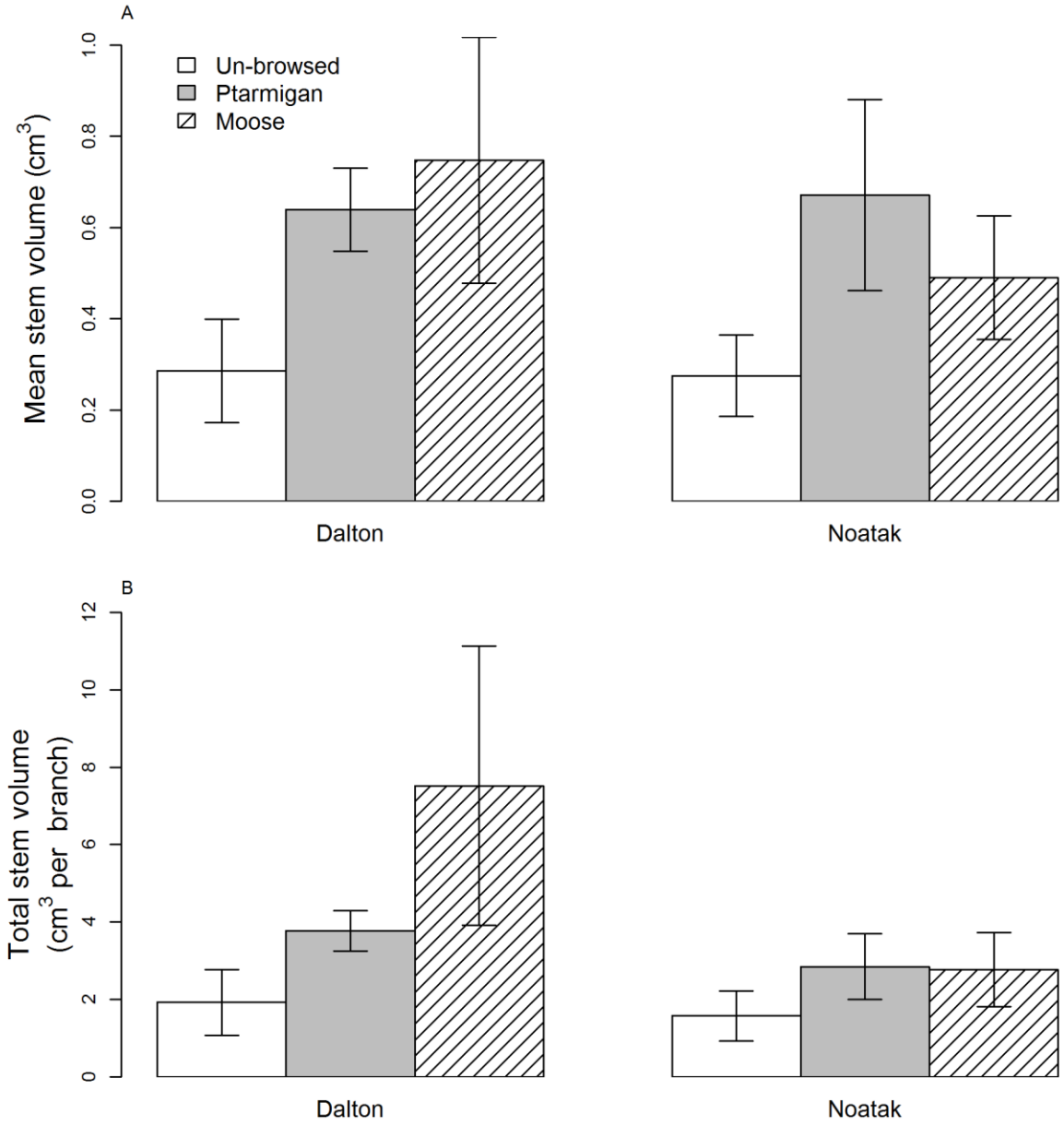

Figure 3-4. Mean (a) and total (b) shoot volume produced during the growing season by feltleaf willows (*Salix alaxensis*) that had been unbrowsed (U), browsed by ptarmigan (*Lagopus lagopus*, *L. muta*; P), or browsed by moose (*Alces alces*; M) the previous winter. Data were collected in 2012 from willows growing in the Noatak and Dalton study areas in northern Alaska. Error bars denote standard error.

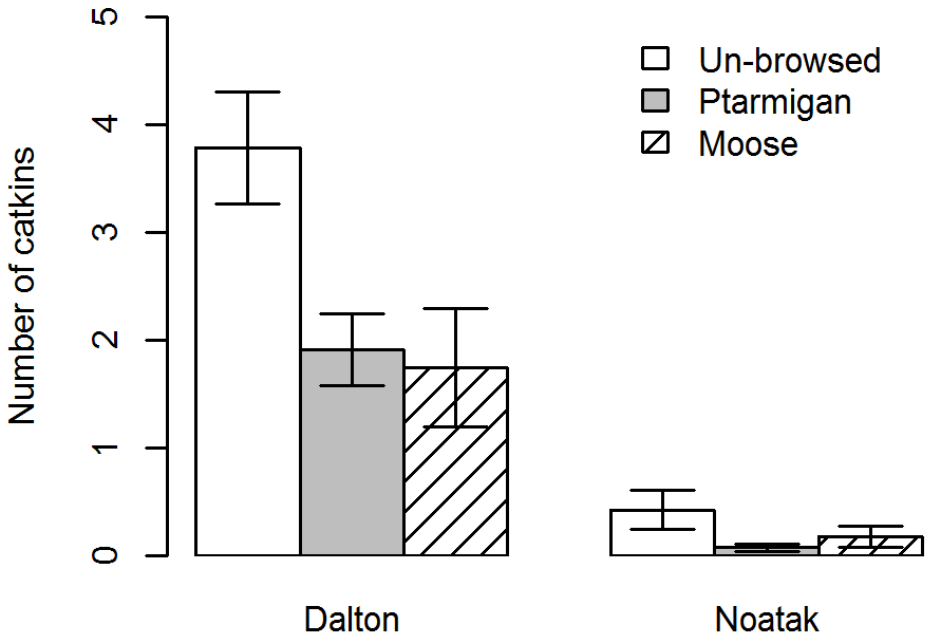

Figure 3-5. Number of catkins per branch of unbrowsed (U), ptarmigan-browsed (*Lagopus lagopus, L. muta*; P), and moose-browsed (*Alces alces*; M) feltleaf willows (*Salix alaxensis*) in the Dalton and Noatak study areas. Error bars denote standard error.

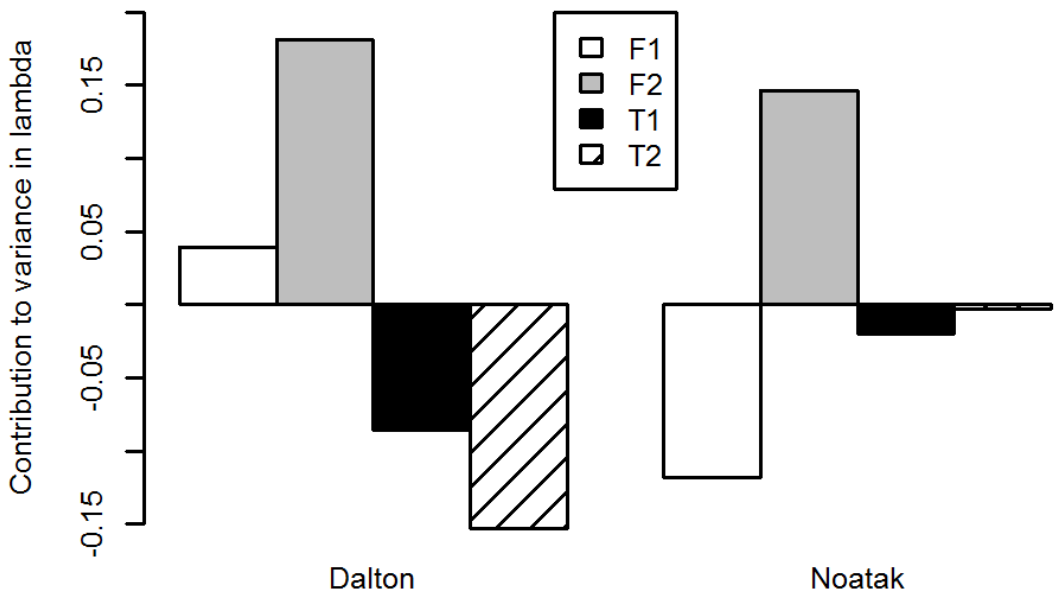

Figure 3-6. Retrospective contributions of matrix elements to variance in bud population growth rates of feltleaf willow (*Salix alaxensis*). F1 is the production of new buds from first-year buds, F2 is the production of new buds from dormant buds, T1 is the probability of transition from first-year bud to a dormant bud, and T2 is the probability that a dormant bud will stay dormant. Positive values reflect an increase in the matrix element in ptarmigan (*Lagopus lagopus, L. muta)* -browsed compared to unbrowsed willows.

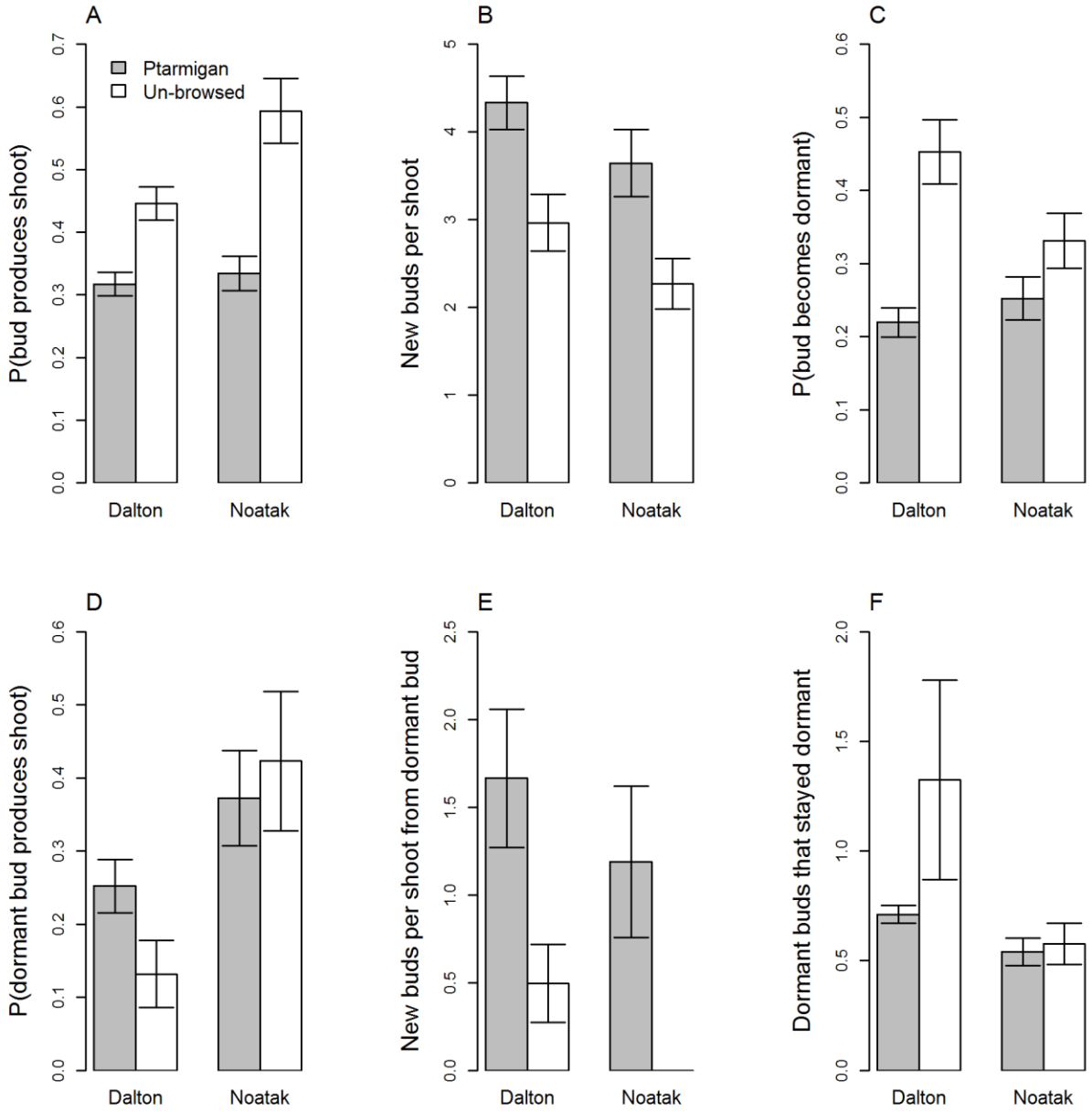

Figure 3-7. Vital rates (and standard errors) of ptarmigan (*Lagopus lagopus*, *L. muta*)-browsed and unbrowsed feltleaf willows (*Salix alaxensis*) in the Dalton and Noatak study areas. Figures A, C, and D reflect probabilities of buds transitioning from one state to another, whereas B, E, and F reflect numbers of buds per shoot. "Dormant buds" are adventitious buds on previous years' growth.

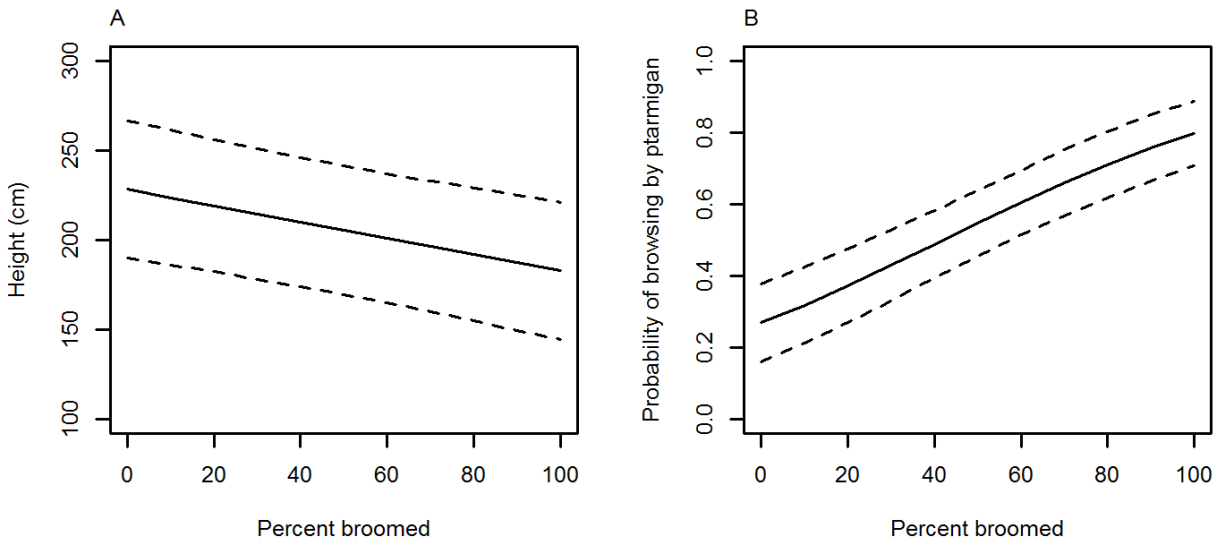

Figure 3-8. Relationship between percent of feltleaf willow (*Salix alaxensis*) branches that were broomed and plant height (a) and the probability of browsing by ptarmigan (b). Mixed models were used to assess the strength of relationships, with proportion of broomed branches as the fixed effect, and site as the random effect. Dotted lines indicate upper and lower 95% confidence intervals.

Figure 3-9. Un-broomed (left) and broomed (right) feltleaf willows (*Salix alaxensis*) in northern Alaska. Ptarmigan (*Lagopus lagopus, L. muta)* tracks are visible around the broomed willow.

3.9 Supporting information

Text S1. Methods used to construct bud matrix population models for browsed and unbrowsed willows and figure depicting the life cycle of buds and vegetative shoots.

Fecundities and transition probabilities (F1, F2, T1, T2) were calculated for two different stages: recently produced buds (hereafter "new buds") and buds that were produced the previous growing season ("dormant buds"). New buds differed from dormant buds by their larger size, fuzzy outer covering, and more apical position on the stem (dormant buds tended to be very small and were positioned at the base of the stem). The production of new buds (F1) from buds was the product of the number of vegetative shoots produced per original bud and the number of new buds produced per vegetative shoot. The production of new buds from dormant buds (F2) was the product of the number of vegetative shoots produced per dormant bud and the number of new buds produced per vegetative shoot. The probability that a bud would transition into a dormant bud (and not become browsed, a catkin, or a vegetative shoot) was determined by dividing the number of buds that became dormant by the total number of buds produced the previous year; T1). The probability that a dormant bud would stay dormant (T2) was calculated as the number of dormant buds that stayed dormant divided by the total number of dormant buds present on the stem the previous year. Mean vital rates (fecundities and transition probabilities) were compared between browsed and un-browsed willows using linear mixed models in program R with browsed/unbrowsed modeled as a fixed effect and site as a random effect. Using these vital rates, we constructed matrices for each browsed and un-browsed willow branch. An average matrix was calculated using the mean parameters for each type of willow branch in each study area, and lambda was calculated as the maximum eigenvalue for each average matrix. We

subsequently calculated retrospective contributions of each parameter (F1, F2, T1, T2) to differences in lambda between browsed and un-browsed plants with a life table response experiment (Caswell 2001) using package “popbio” in program R.

References

Caswell, H. 2001. Matrix Population Models, 2nd edition. Sinauer Associates Inc., Sunderland.

Chapter 4

Experimental evidence that ptarmigan regulate willow bud production to their own advantage[3]

4.1 Abstract

In some ecosystems, vertebrate herbivores increase the nutritional quality and biomass of their food source through repeated grazing, thereby manipulating their environment to support higher densities of animals. We tested whether ptarmigan (*Lagopus lagopus, L. muta*) are capable of regulating the nutritional quality, abundance, and availability of feltleaf willow (*Salix alaxensis*) buds using a simulated browsing experiment and a feeding preference study with wild birds. Simulated ptarmigan browsing resulted in smaller buds, but greater numbers of buds per shoot. Furthermore, browsing altered the morphology of willow branches such that buds were at higher densities and closer to snow level compared to un-browsed controls. Browsing increased the number of willows with accessible buds (buds within 50 cm of snow level) from 55% to 89% of willows, and increased total accessible bud biomass from 113 ± 30 mg to 129 ± 50 mg. Browsing did not affect bud nitrogen or carbon concentration but reduced protein precipitation capacity (tannins) in buds the following winter, indicating that ptarmigan browsing does not induce a defensive response in this species. When branches of broomed (previously browsed) and un-broomed willows were placed in the snow at equal heights, ptarmigan showed no preference for either type; however, they obtained more buds from broomed willows. By increasing the accessibility and density of buds on feltleaf willows, ptarmigan increase the carrying capacity of their habitat, which in turn will support higher densities of ptarmigan.

[3] Prepared for submission to Oecologia as Christie, K.S., and R.W. Ruess. 2014. Experimental evidence that ptarmigan regulate willow bud production to their own advantage.

4.2 Introduction

Many plants have evolved complex chemical and morphological defenses to deter herbivores, yet others remain largely un-defended and consequently lose large quantities of their tissues. These "tolerant" species can be further manipulated by herbivores such that their nutritional quality and productivity is increased (Hilbert et al. 1981; McNaughton 1984; McInnes et al. 1992; Danell et al. 1994). These changes influence the efficiency of browsing, quantity of forage available, and food quality, which in turn can have strong impacts on population dynamics of both plants and herbivores (Fox and Bryant 1984; Hobbs 1996; Person et al. 2003).

Hilbert *et al.* (1981) postulated that as grazing pressure increases, plants can increase, decrease, or have the same productivity relative to ungrazed plants. These responses represent overcompensation, undercompensation, and exact compensation for herbivory, respectively. Aggregations of herbivores have been observed to maintain "grazing lawns", areas where preferred plants are maintained in a state of elevated productivity and palatability through repeated grazing (McNaughton 1984). Both graminoids (Mortimer and Ahlgren 1936; McNaughton 1976; Hik and Jefferies 1990; Person et al. 2003) and shrubs (Wandera et al. 1992; Molvar et al. 1993; Stewart et al. 2006; Fornara and Du Toit 2007) may compensate for herbivory by producing vigorous new growth, and this response is most prevalent in nutrient-rich environments (Harrison and Bardgett 2008). Mechanisms that facilitate compensation include herbivore-related nutrient subsidies via feces and urine, as well as reduced competition for light or nutrients among remaining plant tissues (McNaughton 1983; Rosenthal and Kotanen 1994).

The positive-feedback cycle whereby herbivores maintain or create high-quality resources that benefit future generations has been called "resource regulation" (Craig 1986). If the offspring of an individual herbivore benefit from the induced response of a plant, then selection would favor behavior that induces further plant susceptibility to attack by future generations (Craig 2010). In woody plants, this can occur when herbivory induces vigorous production of new growth and constrains sexual reproduction and senescence, thus perpetuating the juvenile stage of the plant. For example, a bud-galling sawfly (*Euura mucronata*) attack on *Salix cinera* caused surviving buds to produce longer than average shoots, which supported more galls with higher survival rates than control plants (Roininen et al. 1988).

A similar positive-feedback cycle may be occurring between ptarmigan (*Lagopus lagopus, L. muta*) and feltleaf willows (*Salix alaxensis*) in Arctic North America. In the winter and spring ptarmigan concentrate in riparian areas where forage productivity is high and vegetation grows tall enough to exceed snow depth (Irving et al. 1966; Christie et al. 2014a). A major constituent of the winter and spring diet of ptarmigan is feltleaf willow buds (West and Meng 1966). Ptarmigan are capable of significantly altering the growth and architecture of their forage species, and can remove up to 90% of the buds on a single willow (Hakkarainen *et al.* 2007; Tape *et al.* 2010). This species responds favorably to moderate levels of herbivory in the boreal forest, exhibiting increased shoot biomass and nutritional quality of leaves after being browsed by snowshoe hares (Fox and Bryant 1984; Bryant 2003). Possible mechanisms for the observed improvement in food quality after browsing include reduced competition among shoots for resources such as nitrogen, nutrient subsides via feces, and increased allocation of carbon to aboveground growth at the expense of defensive compound production and root growth (Bryant

et al. 1983; Coley et al. 1985, Ruess et al. 1998). When browsed, feltleaf willows appear to employ a "tolerance-escape" strategy common to fast-growing species in resource-rich areas, and allocate resources towards rapid re-growth rather than defense or toughness (Agrawal and Fishbein 2006).Tannins are known carbon-based defensive compounds in willow buds (Wang *et al.* 2011) that can decrease in concentration when browsing induces an over-compensation growth response (Danell and Huss-Danell 1985). However, feltleaf willows are capable of chemically defending tissues when necessary; severe browsing by snowshoe hares induced the production of "stump sprouts" from roots that were well-defended and unpalatable to hares (Bryant *et al.* 1985). Browsing can therefore increase or decrease the nutritional quality of willow tissue depending on the severity of browsing and the chemical response of the plant.

In this study, we evaluated whether ptarmigan regulate the quantity and nutritional quality of buds available for browsing in future years. We build upon a previous study of wild feltleaf willows showing that "broomed" plants with a history of browsing were more likely to be re-browsed by ptarmigan than their un-browsed counterparts (Christie et al. 2014b). We simulated two years of winter ptarmigan browsing on feltleaf willows, and compared the accessibility, abundance, size, and chemical composition of buds produced the third winter between browsed and control plants. We predicted that the loss of apical dominance due to browsing would cause architectural changes (brooming) that would increase the accessibility of buds to ptarmigan the following winter. We anticipated that since it was unlikely that the willows in our experiment were light (and therefore carbon)-limited, browsed willows would increase tannin concentrations in buds to deter further attack by ptarmigan. To evaluate whether ptarmigan preferentially browse and/or obtain more food from willows with a history of browsing, we planted equal

numbers of broomed (with a history of browsing) and un-broomed (not browsed) willow branches in the snow at Arctic field sites and quantified the number and proportion of buds removed by wild ptarmigan.

4.3 Materials and Methods

Simulated browsing

Feltleaf willow (*Salix alaxensis*) cuttings (n=54) were collected from the main stems of healthy wild plants on the University of Alaska Fairbanks campus, and planted inside an electric fence in June 2010. Cuttings were approximately 20 cm in length and 2 cm in diameter, and were planted 30 cm apart. In October 2010, willows were cut to variable heights ranging from 5 – 20 cm for an unrelated study, and left to grow until March 2012. At this time, willows ranged in height from 98-248 cm and had full access to sunlight. Willows were randomly assigned one of two treatments: 1) un-browsed (control); 2) ptarmigan browsing. Simulated ptarmigan browsing consisted of the removal of 70-80% of buds from the distal ends of shoots that protruded above snow level (approximately 65-80 cm deep), resulting in the removal of approximately 30-40% of total buds from each plant. We did not differentiate between vegetative and catkin-producing buds, both of which grow on distal portions of shoots. Our browsing treatment was consistent with observations of ptarmigan browsing intensity on wild willows (Tape et al. 2010; Christie et al. 2014b). In March 2013, we repeated the ptarmigan browsing treatment, and removed 70-80% of buds above the snow. A random subset of seven control plants was harvested at this time for measurements of current annual growth production, leaving 20 control plants and 27 ptarmigan-browsed plants to be harvested in November 2013.

Bud demography and abundance

There are several possible mutually exclusive fates for feltleaf willow buds: they can produce catkins, woody shoots, herbaceous shoots (which die off at the end of the growing season), dormant buds, or they can die of other causes. Buds toward the distal end of the shoot develop into catkins in the early spring, followed by the development of vegetative shoots from apical and axillary buds (Collet 2004). Vegetative shoots produce leaves shortly after budburst. In the late summer, new buds are formed between the leaf petiole and the stem. Buds on the proximal part of the shoot typically do not develop into catkins or shoots and instead become dormant, to be activated if buds at the distal part of the shoot are damaged (Klimesová and Klimeš 2007,). The primary cause of bud death other than browsing in our study was the death of bud-bearing shoots at the base of the main stem, which occurs as the plant increases in height and devotes more resources to shoots in the canopy.

To compare the fate of buds on browsed versus un-browsed willows, bud demography maps were constructed on a random subset of 21 willows (10 control, 11 browsed) in March 2013. For willows with more than one main stem, a random stem was selected and marked with flagging tape. All current shoots (produced during the 2012 growing season) and buds were mapped on paper. Willows were then treated (browsed), and the buds removed were counted and documented on the maps. Catkins were counted on June 12, 2013. In October 2013, the remaining buds were re-mapped, along with new shoots and associated buds that were produced subsequent to the browsing treatment. Also in October 2013, buds on current annual growth (CAG) shoots between heights of 80 and 130 cm were counted to measure the availability of buds to ptarmigan in winter. This height range was chosen so that only buds above snow level

and within easy reach of ptarmigan would be counted. Snow depth at the time of clipping was approximately 65 cm in 2012 and 80 cm in 2013. This is within the range of recorded snow depths (47-138 cm) of Arctic shrub patches (K. Christie, unpublished data).

Bud mass and chemistry

In November and December 2013, willows were harvested, and CAG was freeze dried. Buds were subsequently removed from the terminal ends of 3-4 randomly selected stems (10 buds per stem), weighed, and counted to determine mean bud mass. Because many plants did not produce catkins, this type of bud was not included in the sample to minimize heterogeneity in bud chemistry. Catkins were differentiated from vegetative buds by dissection of the bud. Buds were analyzed for %N and %C in the University of Alaska Fairbanks Forest Soils Lab using a LECO TruSpec CN analyzer. Buds from all remaining stems were analyzed for protein precipitation capacity at the Washington State University Wildlife Habitat and Nutrition Lab using blue-stained bovine serum albumin as a reagent (Martin and Martin 1982; Silber and Davitt 2000).

Feeding preference study

Branches were collected from feltleaf willows growing near the Dalton Highway in northern Alaska between 68.5°N and 69.7°N on 15 April, 2012. We harvested 80 broomed branches and 86 un-broomed branches from willows, and cut each branch to a length of 30-40 cm. We planted branches in the snow so that approximately 25 cm of branch was exposed. Willows were distributed among four existing feltleaf willow stands near the Dalton Highway (same latitudes as above). We collected the willow branches on 20 May, 2012, and counted the number of buds

browsed by ptarmigan (remaining bud scars on the stem indicated where buds had been removed) and the number of buds that remained on the branch. We used this information to calculate total bud density per length of branch and proportion of buds browsed.

Statistical analysis

We used Wilcoxon signed-rank test to assess differences in mass, abundance, fates, and chemistry of buds between experimentally browsed and un-browsed willows (Wilcoxon 1945). For the feeding preference study, we assessed the effect of brooming on the proportion of branches browsed using generalized linear mixed models with a logit link, with "broomed" vs. "un-broomed" as the fixed factor and site as the random factor. Generalized linear mixed models (GLMM's) with a poisson link were used to assess the effect of browse-history on number of buds removed by ptarmigan, and GLMM's with a binomial link were used to assess whether browse-history influenced the proportion of buds browsed. The effect of browse-history on bud density was evaluated using linear mixed models. All analyses were conducted in program R using package lme4 (Bates *et al.* 2013). Package lmerTest was used to calculate p-values for fixed effects in the analysis of bud density (Kuznetsova *et al.* 2014).

4.4 Results

During the ptarmigan browsing treatment we removed approximately 73 ± 1% (SE) of buds above snow level (Table 4-1). As a result of this bud loss, the distal ends of shoots typically died but remained attached to the plant (Fig. 4-1). Apical dominance was interrupted with the removal of terminal buds, and the remaining axillary buds produced live woody shoots, herbaceous

shoots (short leaf-bearing shoots that eventually fell off the plant), dormant buds or buds that died (these buds were usually on dead shoots on the lower part of the main stem). Over time, the production of woody shoots from axillary buds at the distal part of the shoot caused an architecturally complex broomed structure and retarded stem elongation (Fig. 4-1), similar to willows observed in the field (Fig. 4-2). Browsing caused willows to double the proportion of buds that produced woody shoots, resulting in the same number of woody shoots produced on browsed and control plants (Table 4-1, Fig. 4-3). Control plants allocated higher proportions of buds to herbaceous shoots, resulting in eight times the number of herbaceous shoots compared to browsed plants. Proportionately more buds died on browsed plants, but there was no difference in overall numbers of dead buds. No catkins were produced on browsed plants, whereas an average of 1.35 ± 1.14 (SE) catkins were produced per control plant. The browsing treatment did not cause differences in the proportion of buds that became dormant, but the net result was that browsed plants ultimately had less than a third of the number of dormant buds (16 ± 3 buds) per branch compared to control plants (48 ± 7 buds; Table 4-1, Fig. 4-3). We did not observe stump sprouts originating from the root system of browsed or control willows.

Buds were 20% smaller on browsed willows (2.8 ± 0.21 mg) compared to controls (3.5 ± 0.35 mg, $t = 1.74$, p-value = 0.09, Fig. 4-4A) and approximately 40% more buds were produced per shoot on browsed willows than control willows ($t = -3.07$, $p < 0.01$, Fig.4-4B). The number of buds counted within ptarmigan reach (50 cm above snow level) was higher in browsed willows (54 ± 12 buds) compared to controls (34 ± 12 buds, $t = -2.26$, $p = 0.03$; Fig. 4-4C). Approximately 89% of browsed willows produced buds within ptarmigan reach; however, only 55% of control willows produced buds within reach of ptarmigan. The mean biomass of

accessible buds produced by ptarmigan-browsed willows (129 ± 30 mg) was 14% higher than un-browsed controls (113 ± 50 mg; t = -2.23, p = 0.03, Fig. 4-4D).

Simulated browsing caused subtle changes in the chemistry of willow buds. The browsing treatment did not influence the nitrogen concentration of willow buds (Fig. 4-5A, t = -0.13, p-value = 0.89). Mean carbon concentration was also similar between control and browsed willows (Fig. 4-5B, t = 1.42, p-value = 0.17). Protein precipitation capacity was 28% higher in controls (0.010 ± 0.001 mg/mg forage) than browsed willow buds (0.008 ± 0.001 mg/mg forage; t = 1.84, p-value = 0.08, Fig. 4-5C).

When the 166 branches planted in the snow for the feeding experiment were checked after 35 days, three were missing and two were consumed by snowshoe hares (*Lepus americanus*). Of the remaining 161 branches, 73% were browsed by ptarmigan. Before browsing, broomed willows had higher densities of buds than un-broomed willows (Fig. 4-6A; t-value = -2.48, p-value = 0.02). Ptarmigan did not preferentially browse broomed willows (Fig. 4-6B; z-value = 1.03, p = 0.97) but removed more buds from broomed (22 ± 1.6 buds) than un-broomed willows (19 ± 1.3 buds; Fig. 4-6C; z-value = 3.04, p-value < 0.01). The proportion of buds removed by ptarmigan on each type of branch was similar (62% and 66% of buds on un-broomed and broomed branches, respectively; Fig. 4-6D; z-value = -0.621, p-value = 0.53).

4.5 Discussion

This study demonstrates that the removal of buds by ptarmigan alters willow architecture and bud production in such a way that birds receive direct benefits the following winter in the form

of higher bud densities within easy reach. Browsed willows produced more buds per shoot and new shoots grew from axillary buds near the base of old stems, resulting in greater numbers of buds lower down on the plant. This lends support to the hypothesis that by pruning willows and creating browsing "hedges" in feltleaf willow stands (Tape et al. 2010; Christie et al. 2014b), ptarmigan regulate their own food resource (Craig 2010).

The removal of buds on the distal ends of willow shoots changed the fates of the remaining buds. Browsed willows increased the proportion of buds that produced woody shoots so that the plants ultimately produced the same number of woody shoots as un-browsed controls. This came at the cost of producing fewer herbaceous shoots that sequestered carbon during the growing season, and retaining fewer dormant buds that could be stimulated to produce vegetative shoots in case of future damage. The activation of dormant axillary and adventitious buds is an adaptive response of plants to herbivory or environmental damage (Roininen et al. 1988; Carroll and Quiring 2003). Over the long-term, the depletion of this "bud bank" can have a negative effect on the willow's ability to regenerate after further herbivory or other kinds of damage (Klimesová and Klimeš 2007).

Browsed plants produced no catkins and were therefore unable to reproduce sexually. Similarly, wild-browsed felt-leaf willows produced very few catkins (Christie et al. 2014b), providing further evidence that browsing reduces the sexual reproductive capacity of willows. As a result, ptarmigan-browsed willows are likely to depend heavily on asexual reproduction for population growth. Feltleaf willows occur on floodplains and are adapted to frequent physical damage. Other species of floodplain willow readily resprout from stem fragments and can successfully

colonize large areas asexually (Radtke et al. 2011; Budde et al. 2011). However, reduced sexual reproduction may limit dispersal opportunities and result in populations low in genetic diversity. Despite this reduction in fitness, willows may continue to produce vigorous vegetative growth in response to browsing, perhaps indefinitely as long as adequate resources are available (Craig 2010) and browsing intensity is moderate.

The production of long shoots with many buds in response to damage to terminal buds has been observed in other plant-herbivore systems, such as willows parasitized by bud-galling sawflies (Roininen *et al.* 1988) and birch trees browsed by moose (Bergstrom and Danell 1987). The increase in number of buds per shoot, combined with the interruption of apical dominance and formation of new shoots at the proximal rather than terminal end of the stem resulted in greater bud densities and greater biomass of buds within reach of ptarmigan. Buds were smaller on browsed willows, and this may have been due to a tradeoff in resources such that the higher the number of buds per shoot, the smaller the size of each bud. Similar tradeoffs have been observed in the buds of larvae-grazed aquatic plants (Miler and Straile 2010), leaves of angiosperms (Scott and Aarssen 2013) and seeds of woody shrubs (Vaughton and Ramsey 1998).

After two years of simulated browsing, concentrations of carbon and tannins of buds produced the subsequent fall were slightly lower than control plants. In this fast-growing species, the diversion of carbon towards secondary compound production might reduce overall growth potential (Coley *et al.* 1985), and our data indicate that browsed plants were slightly carbon-limited compared with unbrowsed plants. A strong growth response to herbivory is adaptive for feltleaf willows because it allows the plant to sequester large amounts of carbon during the

growing season while compensating for tissue damage by herbivores. Feltleaf willows grow in a disturbance-prone riparian environment where the risk of damage from frequent flooding, shifting ice, and herbivory from birds, mammals, and invertebrates is high. Therefore, a specialized chemical defense response to ptarmigan browsing may not be adaptive. Although feltleaf willows are capable of producing highly-defended stump sprouts (Bryant *et al.* 1985), ptarmigan browsing did not appear to elicit this strong response, and instead reduced the amount of defensive compounds in buds. Protein precipitation capacities of feltleaf willow buds (ranging from 0.002-0.02 mg/mg forage) were low compared with leaves of this species (0.194 mg/mg forage; McArt et al. 2009), suggesting that this willow allocates more resources to defending leaves than buds.

The majority of willows in the feeding trial were browsed by ptarmigan within a three week period, indicating that easily accessible buds may be limiting in the Arctic environment. Ptarmigan are able to feed on buds at the tops of willows, but tend to concentrate their feeding within 30 cm of the snow surface (Tape *et al.* 2010). This may be due to the increased effort required to fly to and balance on upper branches. Ptarmigan did not show a preference or aversion to broomed willow buds, suggesting that browsing-induced chemical changes to buds have a negligible effect on food preference by ptarmigan. However, ptarmigan obtained more buds from broomed willows, which had higher bud concentrations per unit length of branch. Therefore, ptarmigan directly benefited from previous browsing of feltleaf willows.

Our data lend support to the idea that ptarmigan maintain hedges of broomed willows near snow level and prevent them from reaching their maximum growth potential (Tape et al. 2010; Christie

et al. 2014b). We have identified the mechanisms by which ptarmigan browsing increases the susceptibility of willows to further attack, providing evidence for resource regulation (Craig 1986; Price 1991; Craig 2010). As long as willows can re-sprout after browsing, vigorous populations can theoretically be maintained over the long-term, despite the reduction in plant fitness (Craig 2010). If browsing pressure were to increase to unsustainable levels (for example under high ptarmigan densities), willows may not be able to maintain this positive feedback cycle, causing widespread die-off similar to what has occurred with elk over-browsing in Yellowstone National Park (Singer *et al.* 1998) and goose-induced habitat degradation of North American tundra (Peterson *et al.* 2013).

Whether the feeding behavior of an individual ptarmigan directly benefits its offspring thereby enhancing fitness (e.g Roininen *et al.* 1988) is unknown; however, ptarmigan appear to increase the carrying capacity of their habitat similar to savannah ungulates, geese, and elephants (McNaughton 1984; Person et al. 2003; Makhabu et al. 2006). We believe that high resource environments, such as productive feltleaf willow stands growing on the floodplains of northern Alaska and Canada are in an optimal position to support this positive-feedback cycle and therefore high densities of ptarmigan.

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4.7 References

Agrawal A, Fishbein M (2006) Plant defense syndromes. Ecology 87:S132–49.

Bates D, Maechler M, Bolker B, Walker S (2013) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5.

Bergstrom R, Danell K (1987) Effects of simulated winter browsing by moose on morphology and biomass of two birch species. J Ecol 75:533–544.

Bryant JP (2003) Winter browsing on Alaska feltleaf willow twigs improves leaf nutritional value for snowshoe hares in summer. Oikos 1:25–32.

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368.

Bryant JP, Wieland GD., Clausen T, Kuropat P (1985) Interactions of Snowshoe Hare and feltleaf willow in Alaska. Ecology 66:1564–1573.

Budde KB, Gallo L, Marchelli P, et al. (2011) Wide spread invasion without sexual reproduction? A case study on European willows in Patagonia, Argentina. Biol Invasions 13:45–54. doi: 10.1007/s10530-010-9785-9

Carroll AL, Quiring DT (2003) Herbivory modifies conifer phenology: induced amelioration by a specialist folivore. Oecologia 136:88–95. doi: 10.1007/s00442-003-1240-5

Christie KS, Lindberg MS, Ruess RW, Schmutz JA (2014a) Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. Polar Biol. doi: 10.1007/s00300-014-1504-z

Christie K, Ruess R, MS L, Mulder C (2014b) Herbivores influence the growth, reproduction, and morphology of a widespread Arctic willow. PLoS One 9:e101716. doi: doi:10.1371/journal.pone.0101716

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899.

Collet D (2004) Willows of Interior Alaska. U.S. Fish and Wildlife Service, Fairbanks, Alaska.

Craig TP (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. Ecology 67:419–425.

Craig TP (2010) The resource regulation hypothesis and positive feedback loops in plant–herbivore interactions. Popul Ecol 52:461–473. doi: 10.1007/s10144-010-0210-0

Danell K, Bergström R, Edenius L (1994) Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. J Mammal 75:833–844.

Danell K, Huss-Danell K (1985) Terrestrial plant tolerance to herbivory. Oikos 44:75–81.

Fornara DA, Du Toit JT (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. Ecology 88:200–9.

Fox JF, Bryant JP (1984) Instability of the snowshoe hare and woody plant interaction. Oecologia 63:128–135.

Hakkarainen H, Virtanen R, Honkanen JO, Roininen H (2007) Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biol 30:619–624. doi: 10.1007/s00300-006-0221-7

Harrison KA, Bardgett RD (2008) Impacts of grazing and browsing by larger herbivores on soils and soil biological properties. Ecol. Brows. grazing.

Hik ADS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt-marsh forage grass : A test of the predictions of the herbivore-optimization model. J Ecol 78:180–195.

Hilbert ADW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Hobbs NT (1996) Modification of ecosystems by ungulatates. J Wildl Manage 60:695–713.

Irving L, West C, Peyton LJ, Paneak S (1966) Migration of willow ptarmigan in arctic Alaska. Arctic 20:77–85.

Klimesová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessment. Perspect Plant Ecol Evol Syst 8:115–129. doi: 10.1016/j.ppees.2006.10.002

Kuznetsova A, Brockhoff PB, Haubo R, Christensen B (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-6.

Makhabu SW, Skarpe C, Hytteborn H (2006) Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. Acta Oecologica 30:136–146. doi: 10.1016/j.actao.2006.02.005

Martin JS, Martin MM (1982) Tannin assays in ecological studies: lack of correlation between phenolics , proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia 54:205–211.

McArt SH, Spalinger DE, Collins WB, et al. (2009) Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400–11.

McInnes PF, Naiman RJ, Pastor J, Cohen Y (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale. Ecology 73:2059–2075.

McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92–94.

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886.

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

Miler O, Straile D (2010) How to cope with a superior enemy? Plant defence strategies in response to annual herbivore outbreaks. J Ecol 98:900–907. doi: 10.1111/j.1365-2745.2010.01674.x

Molvar EM, Bowyer RT, Van Ballenberghe V, Van Brauenberone V (1993) Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479.

Mortimer GB, Ahlgren HL (1936) Influence of fertilization, irrigation, and stage and height of cutting on yield and composition of Kentucky blue-grass. J Am Soc Agron 28:515–533.

Person BT, Herzog MP, Ruess RW, Sedinger JS (2003) Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592. doi: 10.1007/s00442-003-1

Peterson SL, Rockwell RF, Witte CR, Koons DN (2013) The legacy of destructive snow goose foraging on supratidal marsh habitat in the Hudson Bay lowlands. Arctic, Antarct Alp Res 45:575–583.

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251.

Radtke A, Mosner E, Leyer I (2011) Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss. Plant Biol 14:257–64. doi: 10.1111/j.1438-8677.2011.00509.x

Roininen H, Price PW, Tahvanainen J (1988) Field test of resource regulation by the bud-galling sawfly, *Euura mucronata*, on *Salix cinerea*. Holarct Ecol 11:136–139. doi: 10.1111/j.1600-0587.1988.tb00791.x

Rosenthal JP, Kotanen PM (1994) Terrestrial plant tolerance to herbivory. Trends Ecol Evol 9:145–8. doi: 10.1016/0169-5347(94)90180-5

Ruess RW, RL Hendrick, JP Bryant (1998) Regulation of fine root dynamics by mammalian browsers in early successional Alaskan Taiga Forests. Ecology 79: 2706-2720.

Scott SL, Aarssen LW (2013) Leaf size versus leaf number tradeoffs in dioecious angiosperms. J Plant Ecol 6:29–35. doi: 10.1093/jpe/rts029

Silber M, Davitt B (2000) Preparative binding of coomassie brilliant blue to bovine serum albumine at alkaline pH. Prep Biochem Biotechnol 30:209–229.

Singer FJ, Zeigenfuss LC, Cates RG, et al. (1998) Elk, multiple factors, and persistence of willows in National Parks. Wildl Soc Bull 26:419–428.

Stewart KM, Bowyer RT, Ruess RW, et al. (2006) Herbivore optimization by North American Elk: consequences for theory and management. Wildl Monogr 167:1–24.

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186–193. doi: 10.2980/17-2-3323

Vaughton G, Ramsey M (1998) Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). J Ecol 86:563–573.

Wandera AJL, Richards JH, Mueller RJ (1992) The relationships between relative growth rate , meristematic potential and compensatory growth of semiarid-land shrubs. Oecologia 90:391–398.

Wang J, Fang Y, Klaus S, Sun Y-H (2011) Winter foraging strategy of the Chinese Grouse (*Bonasa sewerzowi*): ecological and physiological factors. J Ornithol 153:257–264. doi: 10.1007/s10336-011-0717-y

West G, Meng M (1966) Nutrition of willow ptarmigan in northern Alaska. Auk 83:603–615.

Wilcoxon F (1945) Individual comparisons by ranking methods. Biometrics Bull 1:80–83.

4.8 Figures

Figure 0-1. Un-browsed (left) and ptarmigan-browsed (right) *Salix alaxensis* stems after 1 year of simulated browsing.

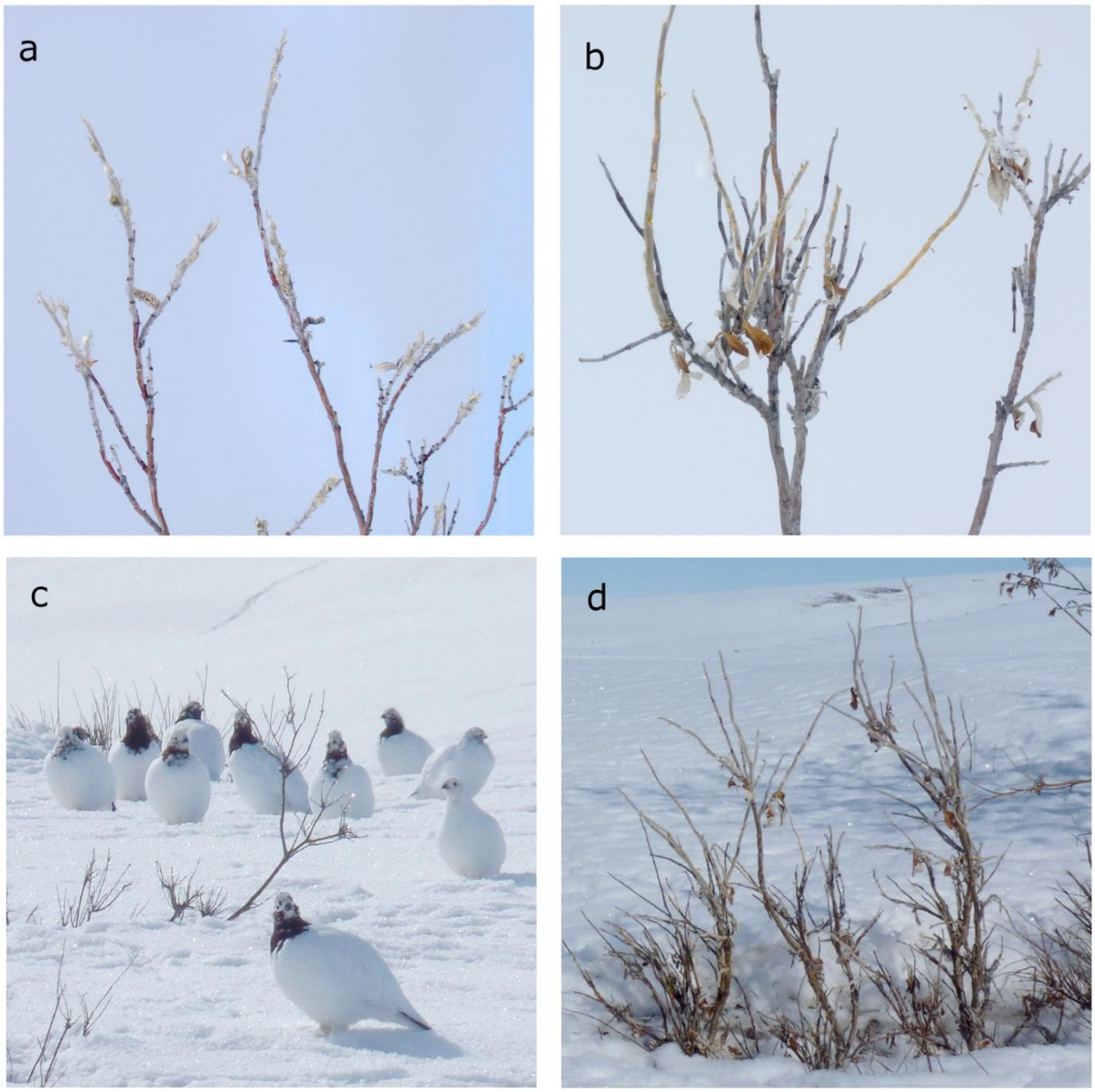

Figure 0-2. Photos depicting a) un-broomed feltleaf willow branches b) broomed feltleaf willow branches showing scars where buds and bark have recently been removed by ptarmigan, c) willow ptarmigan near broomed willows, d) heavily broomed feltleaf willows.

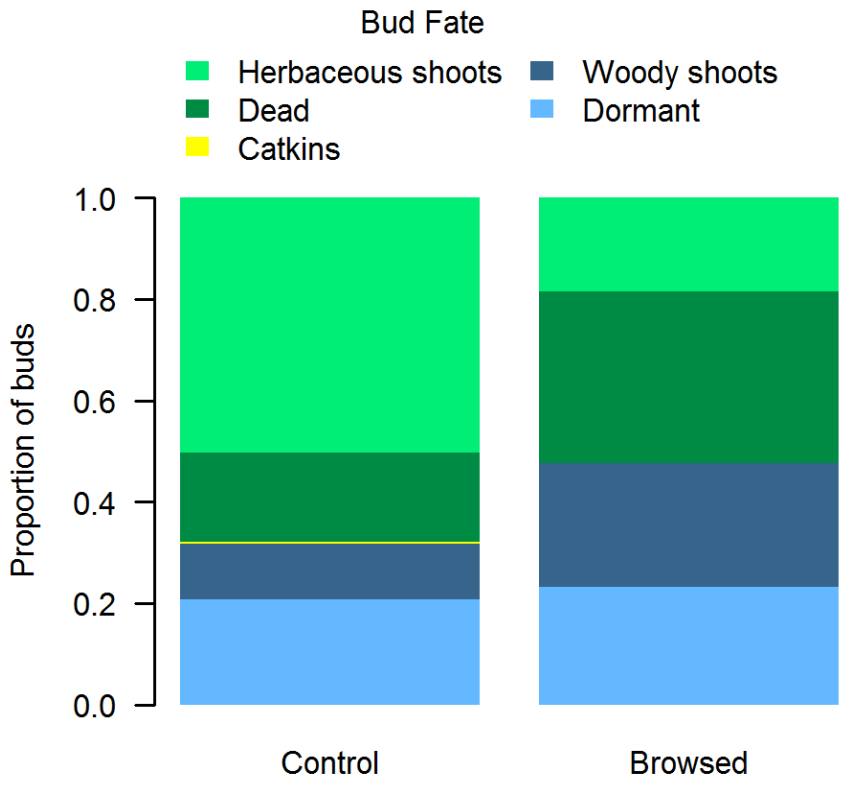

Figure 0-3. The fates of remaining buds on experimentally browsed and control feltleaf willows (*Salix alaxensis*). Approximately 73% of buds were removed from treatments. Buds were counted and marked in March before the browsing treatment, and their fates were determined the following October.

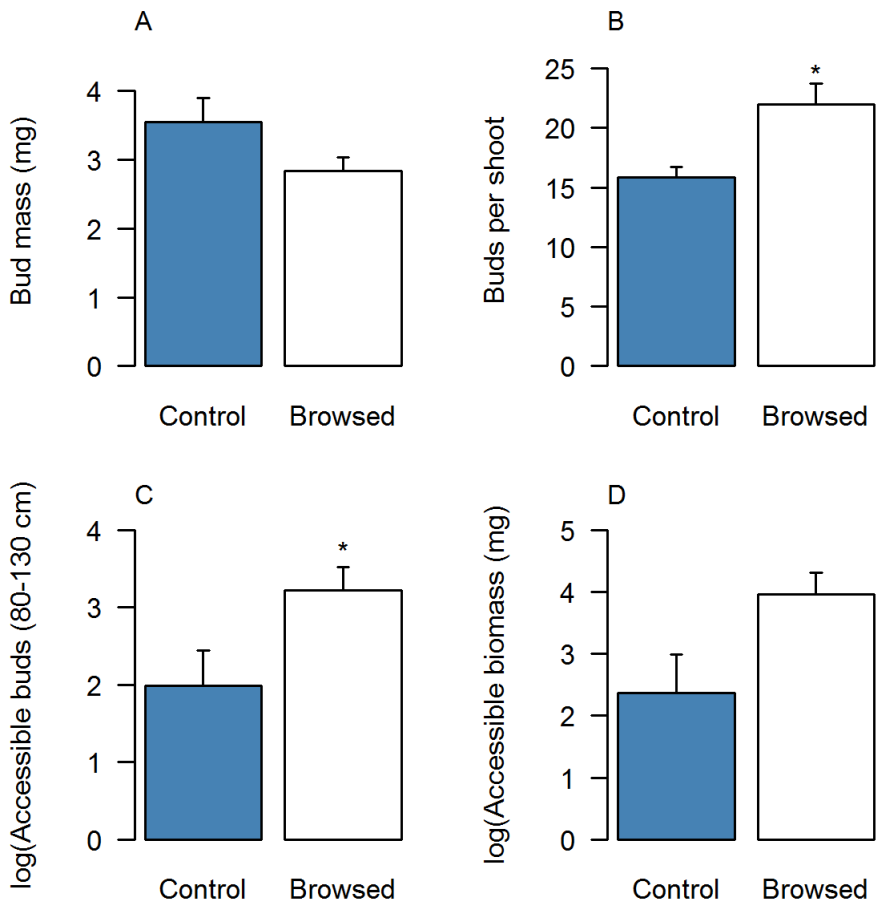

Figure 0-4. Mean and standard error of a) bud mass (mg dry weight), b) buds per shoot, c) number of accessible buds between heights of 80 and 130 cm (within easy reach of ptarmigan foraging on the snow) and d) total accessible bud biomass on feltleaf willows (*Salix alaxensis*) that were experimentally browsed by ptarmigan. Accessible buds and biomass are shown on the log scale. Asterisks denote a significant difference between control and browsed willows at an alpha-level of 0.05.

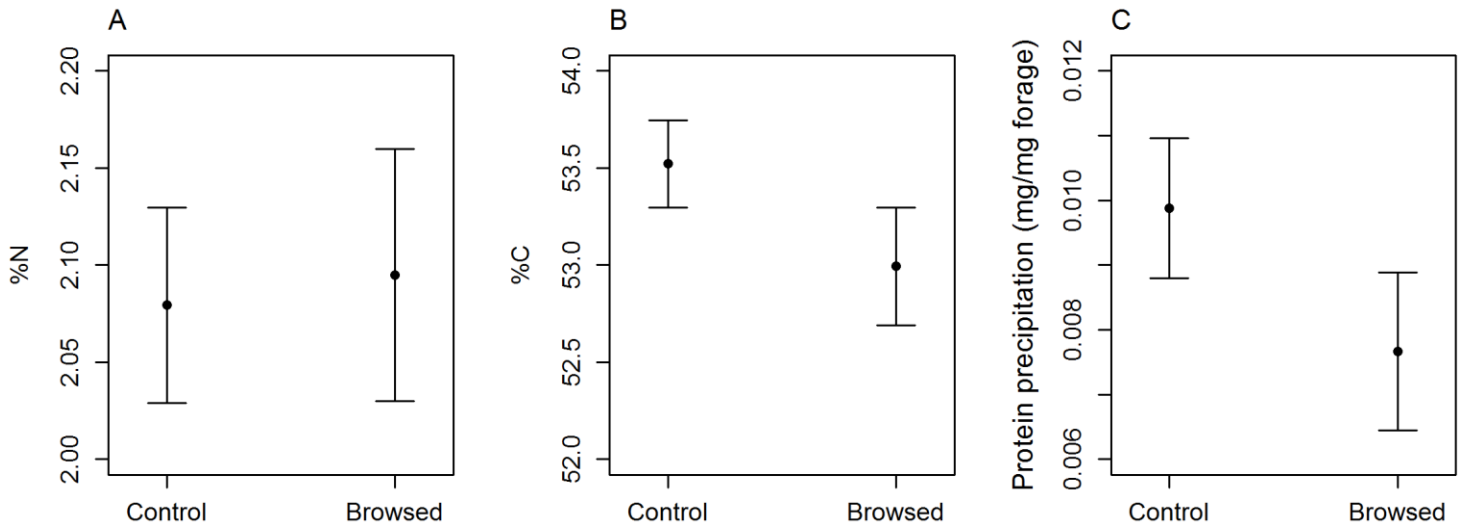

Figure 0-5. a) Mean and standard error of percent nitrogen, b) carbon, and c) protein precipitation in control and browsed feltleaf willow (*Salix alaxensis*) buds. Protein precipitation was quantified as mg BSA (bovine serum albumin) per mg dry forage material (buds).

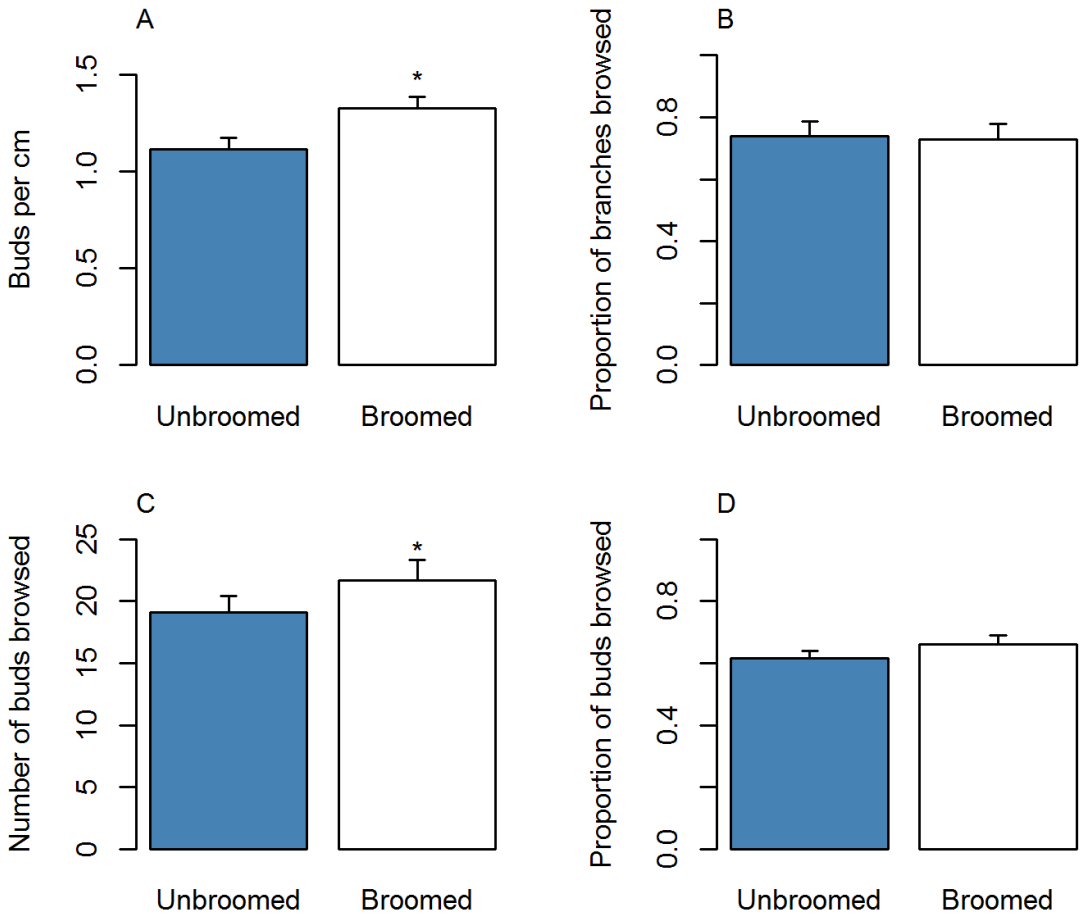

Figure 0-6. Results of feeding preference study, where un-broomed (no history of browsing) and broomed (history of browsing) feltleaf willows (*Salix alaxensis*) were planted in the snow and browsed by wild ptarmigan in northern Alaska. Shown are a) bud densities, b) proportion of branches browsed by ptarmigan, c) number of buds browsed by ptarmigan, and d) proportion of buds on each branch browsed by ptarmigan. Error bars represent standard errors. Asterisks denote a significant difference between control and browsed willows at an alpha-level of 0.05.

4.9 Tables

Table 4-1.The fates of buds of browsed and un-browsed feltleaf willows (*Salix alaxensis*) one year after browsing. Fates are shown as proportions of remaining buds and number of buds or shoots per branch. Differences between browsed and un-browsed willows were tested using non-parametric Wilcoxon signed-rank tests.

	Proportion of buds			Number of buds or shoots		
	Control	Browsed	p	Control	Browsed	p
Woody shoots	0.11 ± 0.01	0.24 ± 0.03	0.003	25.30 ± 17.64	17.64 ± 2.74	0.148
Dormant buds	0.21 ± 0.02	0.23 ± 0.04	0.557	48.10 ± 7.43	15.64 ± 3.40	< 0.001
Catkins	0.00 ± 0.00	0.00 ± 0.00	0.064	1.35 ± 1.14	0	0.064
Dead buds	0.18 ± 0.04	0.34 ± 0.07	0.091	38.4 ± 7.26	29.36 ± 9.18	0.218
Herbaceous shoots	0.50 ± 0.03	0.19 ± 0.04	< 0.001	117.65 ± 16.90	14.55 ± 3.27	< 0.001
Sample size	10	11	-	10	11	-

Chapter 5

The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis[4]

5.1 Abstract

Shrubs have been expanding in Arctic ecosystems over the past century, and herbivores are likely influencing and responding to this expansion. The degree to which herbivores influence shrubs varies by species-specific palatability and tolerance to herbivory, as well as herbivore density. Deciduous shrubs are generally faster-growing and respond more rapidly to improved conditions in the Arctic; however, they are also preferred by herbivores and may be at a disadvantage compared to evergreen shrubs that are avoided by herbivores. This study synthesizes new and existing data from observational and experimental studies to examine how vertebrate herbivores differentially influence shrub species to modify community composition in the Arctic. Our data on winter browsing by ptarmigan (*Lagopus lagopus*, *L. muta*), moose (*Alces alces*), snowshoe hares (*Lepus americanus*), and small mammals shows that large differences in browsing pressure exist within the deciduous shrub community in northern Alaska, where willows are consumed more frequently and intensely than dwarf resin birch (*Betula nana exilis*) and Siberian alder (*Alnus viridis fruticosa*). Studies generally support the idea that willows (*Salix* spp.) and non-resin birches (*B. nana* ssp. *nana*) are more heavily regulated by herbivores than less palatable dwarf resin birch, Siberian alder, and evergreen shrubs, although the latter can be impacted by high herbivore densities. Long-term studies of vegetation change in the Arctic show that deciduous shrubs have spread more rapidly than evergreen shrubs in most regions, so it appears that deciduous shrub expansion is tempered but not prevented by herbivores.

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Unpalatable but fast growing species such as Siberian alder likely have a strong advantage over other species like willows and are expected to expand more quickly. As boreal herbivores expand into Arctic ecosystems in response to changing environmental conditions, they will play an increasingly important role in influencing shrub expansion.

5.2 Introduction

Climate warming in the Arctic has caused the rapid expansion of woody shrubs over the past half-century (Chapin et al. 1995; Sturm et al. 2001; Walker et al. 2006; Tape et al. 2006) and herbivory has been widely recognized as one of the key factors influencing this expansion (Myers-Smith et al. 2011). Vertebrate herbivores are capable of strongly regulating the rates of vegetation change in tundra ecosystems, and the number of studies on the topic has increased in recent years. The need to understand plant-animal interactions in a warming Arctic has prompted exclosure experiments and observational studies demonstrating that herbivores can curtail the expansion of their preferred species (Gough et al. 2007; Post and Pedersen 2008; Olofsson et al. 2009; Speed et al. 2010). For example, the aboveground biomass responses of dwarf birch (*Betula nana nana*) and gray-leaf willow (*Salix glauca*) to increased temperature were reduced substantially when plants were browsed by caribou and muskoxen (Post and Pedersen 2008).

Despite the known importance of herbivores in regulating the response of tundra shrubs to climate change, uncertainty exists as to the degree to which different shrub species and assemblages are influenced by climate change and herbivory. The response of shrubs to climate change is a function of their innate growth rate, how they respond to altered conditions (such as

longer growing seasons, greater nutrient availability, soil disturbance), and site characteristics (Myers-Smith *et al.*, 2011; Tape *et al.*, 2012). The counteracting effect of herbivory on shrubs will vary according to browsing pressure, plant palatability, plant tolerance to herbivory and capacity for regrowth, and resource availability (Mulder, 1999; Wise & Abrahamson, 2007; Speed et al., 2010; Myers-Smith et al., 2011).

An initial step in understanding how woody shrub species are differentially affected by herbivores is to document rates of herbivory across functional groups, or groups that share morphological, physiological, or phenological traits (Pérez-Harguindeguy et al. 2003; Díaz et al. 2004). The Arctic shrub community can be divided most simply into two distinct functional groups, deciduous and evergreen shrubs, which have different traits that control both their response to environmental change and herbivory (Chapin et al. 1996). Size, relative growth rate, patterns of resource partitioning, and the ability to persist following disturbance are traits that influence how a plant will respond to environmental change. Deciduous plants tend to have high growth rates and high carbon demands, and as a result partition a high proportion of growth to leaf area (Chapin et al. 1996, Hobbie and Chapin 1998). This group invests in the acquisition rather than the conservation of resources (Díaz et al. 2004; Wright et al. 2004) and tends to be poorly defended by secondary metabolites and thus more palatable to herbivores compared to evergreen species (Coley et al. 1985; Mulder 1999; Pérez-Harguindeguy et al. 2003). As conditions in the Arctic improve for plants (e.g. longer growing seasons, increased soil temperature and nutrient availability, increased solar radiation, altered soil moisture regimes, soil disturbance, and timing of snow melt (Myers-Smith et al. 2011), fast-growing, palatable deciduous shrubs are expected to respond most rapidly, thereby providing more food for

herbivores (Chapin et al. 1996). Tall deciduous shrubs such as willows (*Salix* spp.) and alder (*Alnus* spp.) may have an advantage over dwarf shrubs because their exposure above the snow allows for early leaf-out and reproduction during warm spring conditions and promotes earlier snow melt (Pomeroy et al. 2006). However, they also lack the protection that snow provides against extreme freeze-thaw cycles, herbivores, and wind (Myers-Smith et al. 2011). In contrast, slow-growing evergreen shrubs have thick, well-defended leaves, tend to occupy more nutrient-poor sites with minimal disturbance, and are expected to respond more slowly to climate change (Chapin et al. 1996). Deciduous shrubs have been expanding in tundra regions (Sturm *et al.*, 2001; Tape *et al.*, 2006; Forbes *et al.*, 2010) and evidence suggests they respond more readily to warming experiments than evergreen shrubs (Wahren et al. 2005; Daniëls et al. 2011; Gough et al. 2012; but see Zamin et al. 2014 and Hudson et al. 2011). The range expansion of poorly-defended deciduous shrubs such as willows and non-resin birches (e.g. *Betula nana nana*) is expected to be more strongly inhibited by herbivores than shrubs that are better defended (Bryant et al. 2014). However, there is evidence that the biomass of largely unpalatable ericoid shrubs can be greatly reduced by herbivores because even a small amount of tissue removed from an evergreen shrub has a large impact on growth rates relative to un-browsed shrubs (Dahlgren et al. 2009; Olofsson et al. 2014).

The intensity of herbivory strongly influences the degree to which shrub communities are impacted by browsing. At low or moderate levels of herbivory, tolerant plants often increase growth rates and decrease secondary compound concentrations relative to ungrazed plants (Hilbert *et al.*, 1981; McNaughton, 1983). This results in the creation of "grazing" or "browsing lawns" where herbivores increase the amount and quality of their food source and tolerant

species remain dominant (McNaughton 1984; Guillet and Bergstrom 2006; Christie et al. 2014a). However, at high intensities of browsing, the loss of tissue cannot be sustained and NPP decreases, facilitating community shifts towards less palatable species (Singer et al. 1994; Butler and Kielland 2008). Resource availability will dictate whether a plant will exhibit tolerance to herbivory; for example, leaf herbivory that affects photoassimilation of carbon will have a more severe effect on shaded plants than those with access to full sunlight (Wise and Abrahamson 2007). Therefore, the effects of herbivores will be most pronounced in regions where herbivores are at high densities and influence resources that are already limiting in plants.

This review will synthesize evidence from Arctic-wide studies of herbivory and shrub expansion, and will review the degree to which herbivores, whose ranges and abundances are also responding to climate change, reduce or inhibit responses of different woody shrub species to climate change. It will address the following key questions: 1) How do Arctic shrub species differ in defensive compound production and palatability to herbivores? 2) Is there evidence that palatable deciduous shrubs are more strongly inhibited (i.e., growth rates are reduced compared to un-browsed plants) by herbivores than less-palatable evergreen shrubs? 3) Are deciduous shrubs expanding more rapidly than evergreen shrubs, or vice versa? 4) What role do herbivores play in facilitating the expansion of non-preferred species? We will combine evidence from existing observational and experimental studies with original data on herbivory in northern Alaska to answer these questions.

5.3 Variation in the palatability of Arctic shrubs

The palatability of shrubs to herbivores is dependent on the amounts of carbon-based defensive compounds (e.g. toxins and protein precipitating compounds), nutrients, lignin, and cellulose in plant tissues, as well as the relative palatability of other available plants (Bryant and Kuropat 1980; Mattson 1980; Palo 1985). Nevertheless, broad generalizations about plant groups can be made, representing a continuum of growth/defense tradeoffs (Bryant et al. 1983; Coley et al. 1985). In general, fast-growing species in disturbed areas, such as willows, are the least chemically-defended group of shrubs, while slower growing dwarf evergreen shrubs have the highest concentrations of defensive compounds. Evergreen ericoids such as *Empetrum nigrum* and *Vaccinium vitis-idaea* typically accumulate high concentrations of phenolics, which inhibit the digestion of protein in animals (Iason and Palo 1991). However, levels in plant tissues are known to vary seasonally, annually, and regionally (Jung et al. 1979; Jonasson et al. 1986; Nilsson et al. 1998; Hansen et al. 2006). In addition to phenolics, leaves of evergreen ericoid shrubs contain other unpalatable components such as support structures and thick, waxy cuticles (Dahlgren et al. 2009). For this reason, these shrubs are generally avoided by herbivores (White & Trudell, 1980; Dahlgren *et al.*, 2007; Rammul *et al.*, 2007; Table 5-1). Conversely, the leaves of deciduous ericoid shrubs such as *Vaccinium myrtillus* are preferred foods for hares, voles, and ptarmigan (Stokkan & Steen, 1980; Hjältén *et al.*, 2004; Dahlgren *et al.*, 2007, 2009; Pedersen *et al.*, 2011; Table 5-1). This may be because their leaves contain fewer secondary metabolites such as phenolics and/or higher nitrogen concentrations compared to evergreen shrubs (Dahlgren et al. 2009; Kaarlejärvi et al. 2012).

Betula nana (dwarf birch) is a dwarf deciduous shrub distributed throughout the circumpolar Arctic consisting of two sub-species with different concentrations of secondary metabolites (Bryant *et al.*, 1989, 2014; Table 5-1). The non-resinous sub-species, *B. nana nana*, occurs in Fennoscandia, Iceland, Greenland, and eastern Canada, whereas the resinous *B. nana exilis* occurs in Siberia and western North America (Graglia et al. 2001; Bryant et al. 2014). *B. nana exilis* twigs are lined with resin glands, which produce highly toxic triterpenes such as papyriferic acid (Bryant et al. 1989; Bryant et al. 2014). Geographical differences in defense within the same or closely related species are thought to be due to differences in herbivore density (Burns 2014, Bryant et al. 1994). *B. nana exilis* is rarely browsed by caribou (*Rangifer tarandus),* muskox (*Ovibos moschatus),* or voles (*Microtus oeconomus,* and *M. miurus)* in North America (Kuropat 1984; Batzli and Lesieutre 1991; Larter and Nagy 1999) and is less palatable to snowshoe hares than *B. nana nana* (Bryant et al. 1989). However, *B. nana exilis* buds are consumed by ptarmigan (Weeden 1969). *B. nana nana* is browsed by reindeer (Olofsson et al. 2009) and gray-sided voles, although the latter only consume it when their preferred forage has been depleted (Dahlgren *et al.*, 2007; Table 5-1). Although it has fewer resins than its North American/Siberian counterpart, *B. nana nana* has higher concentrations of phenolics than *B. nana exilis* and ericoid shrubs such as *V. myrtillus, V. vitis-idaea,* and *E. hermaphroditum* (Bryant et al. 1989; Kaarlejärvi et al. 2012).

Similar to *B. nana exilis*, the resinous *B. glandulosa* (tall shrub birch) is defended by toxic triterpenes (Bryant et al. 2014). However, this deciduous shrub, found in North America and Greenland, is frequently consumed by ptarmigan (Montgomerie and Holder 2008) and is preferred over other shrubs by snowshoe hares (Smith et al. 1988). It is considered an

unimportant food source for moose (Paragi et al. 2008) and a marginally important food source for caribou (Manseau *et al.*, 1996; Crete & Doucet, 1998; Table 5-1). However, limited information about the palatability of this species relative to other shrubs prevents strong inferences about herbivore preference.

Alnus viridis fruticosa (Siberian alder) is a tall deciduous nitrogen-fixing shrub that defends its twigs and buds with resins containing the highly toxic stilbenes pinosylvin (PE) and pinosylvin methyl ether (PME) as well as other phenols, which are very likely toxic if ingested in high quantities (Bryant *et al.*, 1983, Clausen et al. 1986, Table 5-1). Snowshoe hares consume alder internodes containing phenols, but spit out the buds containing PE and PME, suggesting that these stilbenes are more toxic to hares than other phenols (Bryant et al. 1983, Clausen et al. 1986). Most northern vertebrates avoid browsing Siberian alder, but a number of different invertebrates are known to attack this shrub (Hendrickson et al. 1991; Hjältén and Palo 1992; Mulder et al. 2008). Alder is unique on the tolerance-defense spectrum, with its ability to invest in rapid growth and highly effective anti-browsing defense, which are a consequence of its capacity to fix nitrogen and intolerance to browsing (Hendrickson et al. 1991).

Willows are not well-defended in comparison to alder, birch, and evergreen ericoid shrubs, but willows are a highly diverse group, containing varying concentrations of phenolic glycosides, flavonoids, and polyphenols (Bryant et al. 1989; Hansen et al. 2006; Heiska et al. 2007). Willows are browsed by many, if not all, Arctic herbivores, including mountain hares (*Lepus timidus*), snowshoe hares, ptarmigan, caribou and reindeer (*Rangifer tarandus*), moose, muskox (*Ovibos moschatus*), lemmings (*Lemmus* spp.), voles (*Microtus* spp.), and ground squirrels (*Urocitellus*

parryii; Batzli & Sobaski, 1980; Bryant *et al.*, 1989; Batzli & Lesieutre, 1991; Predavec & Danell, 2001; Tolvanen *et al.*, 2002; Hakkarainen *et al.*, 2007; Berg *et al.*, 2008; den Herder *et al.*, 2008; Pajunen *et al.*, 2008; Tape *et al.*, 2010; Figure 5-2). Many willow species exhibit remarkable tolerance to herbivory through strong compensatory growth responses (Danell et al. 1994; Skarpe and van der Wal 2002; Bowyer and Neville 2003; Christie et al. 2014a); however, a gradient of tolerance versus defensive traits exists within the genus. Similar to trends observed in *B. nana*, European willows (*S. caprea* and *S. phylicifolia*) have lower concentrations of secondary metabolites and are more palatable to hares than willows that occur in similar habitats in North American and Siberia (*S. alaxensis* and *S. arbusculoides*; Bryant *et al.* 1989). Palatability to herbivores can vary within a species, and even within the lifespan of an individual willow. For example, *S. alaxensis* juvenile "stump sprouts" are much more heavily defended than adult plant tissues (Fox and Bryant 1984). Willows also exhibit strong intra-seasonal variability, with the highest concentrations of toxic phenolic glycosides in the bark observed during the dormancy period (Hansen et al. 2006; Förster et al. 2010).

5.4 Defensive compounds and climate change

Increased temperatures and nutrient availability in Arctic regions are expected to favor fast-growing deciduous shrubs over less-palatable evergreen shrubs (Chapin *et al.*, 1995; Bret-Harte *et al.*, 2008; Elmendorf *et al.*, 2012), although measurable changes in species composition do not always occur in experimentally warmed sites (Kaarlejärvi et al. 2012). Willows are adept at responding positively to improved conditions in the Arctic (Walker 1987; Pajunen 2009; Forbes et al. 2010; Myers-Smith et al. 2011), and the spread of willows may lead to an overall increase in palatability of Arctic shrub communities. The observed increase in abundance of the largely

unpalatable Siberian alder across the Arctic is a notable exception to this trend (Sturm et al. 2001; Tape et al. 2006; Frost and Epstein 2014), and the high concentrations of secondary metabolites in its tissues may be indirectly facilitating its expansion through reduced rates of herbivory.

When exposed to warmer temperatures or nutrient addition, shrubs are expected to decrease concentrations of secondary metabolites and instead invest carbon in the production of new growth (Coley et al. 1985). Growth responses to warming and fertilization treatments, however, do not always support this theory, and appear to be highly species and context-specific. In support of this theory, both *B. nana nana* and *B. nana exilis* decreased condensed tannin concentrations after fertilization (Graglia et al. 2001). Similarly, fertilization caused *S. herbacea x polaris* to reduce concentrations of condensed tannins in leaves (Hansen et al. 2006). However, in the same experiment, *V. vitis-idaea* increased concentrations of tannins after warming and nutrient addition. In a separate study, warming had little or no effect on tannin concentrations in *E. hermaphroditum*, *V. vitis-idaea*, *V.myrtillus* or *B. nana nana* (Kaarlejärvi et al. 2012).

5.5 Variation in susceptibility to herbivory within the Arctic shrub community – A case study

To determine whether the continuum of tolerance versus defense within the Arctic shrub community explains herbivore preference and foraging intensity, we surveyed six Arctic woody shrub species (*Salix alaxensis*, *S. lanata*, *S. pulchra*, *S. glauca/niphoclada*, *B. nana exilis*, *Alnus viridis fruticosa*) for signs of browsing. See supporting information for details about data collection. *S. glauca* and *S. niphoclada* were impossible to differentiate at some of our sites and

were therefore grouped. The production of defensive compounds pinosylvin methyl ether and toxic triterpenes by *A. viridis* and *B. nana*, respectively, is likely to deter many herbivores (Bryant et al. 1983; Bryant et al. 1989; Bryant et al. 2014). Our data generally supported this prediction. Moreover, a gradient of herbivory existed within the willow genus, confirming that willow species vary in their palatability to herbivores (Figure 5-3). *S. alaxensis*, and to a lesser extent the other willow species, were heavily browsed by ptarmigan, moose, and small mammals (Figure 5-3). *B. nana* was browsed by ptarmigan and small mammals, whereas *A. viridis* was avoided by moose and ptarmigan, but browsed by small mammals and snowshoe hares (Figure 5-3). When all herbivores were combined, *S. alaxensis* was browsed most frequently (84% of willows were browsed), followed by other willow species (50-71%), *A. viridis* (50%), and lastly, *B. nana* (38%). Browsing intensity (proportion of stems browsed) followed the same pattern and was greatest for *S. alaxensis* (46%), followed by *S. pulchra* (37%), *S. glauca/niphoclada* (26%), *S. lanata* (24%), *A. viridis* (19%), and *B. nana* (17%, Figure 5-4).

In summary, patterns of herbivory by ptarmigan and moose largely adhered to the continuum of tolerance versus defense, with willows experiencing the greatest levels of herbivory and alder and birch experiencing the least. Snowshoe hares and small mammals did not show strong preferences, and fed on greater amounts of alder and birch than the other herbivores. These results indicate herbivore-specific foraging strategies, which will in turn dictate their role in shaping Arctic shrub communities. When herbivores were combined, willows were more frequently and intensively browsed than other deciduous shrubs. This has strong ramifications for expanding shrub communities. *B. nana exilis* and *A. viridis* may have an advantage over heavily browsed species such as *S. alaxensis* if they are able to increase growth rates in response

to warmer conditions. However, willows are known for their resilience to herbivory, and may be able to compensate for herbivory if adequate resources are available (Wandera *et al.*, 1992; Molvar *et al.*, 1993; Stewart *et al.*, 2006; Fornara & Du Toit, 2007, Christie et al. 2014a).

5.6 Evidence for the regulation of shrub expansion by herbivores

Evergreen shrubs are expected to respond more slowly to climate change than deciduous shrubs due to their inherently slow growth rates (Chapin et al. 1996). An analysis of 11 warming experiments at International Tundra Experiment sites across the tundra biome showed that deciduous shrubs increased height and cover to a greater extent than evergreen shrubs when temperatures were increased by 1-3°C (Walker et al. 2006). A meta-analysis of 61 warming experiments across the Arctic further supported this idea (Elmendorf et al. 2012). However, evergreen shrubs in experimentally warmed chambers have been shown to rapidly increase their biomass relative to controls in low-productivity areas where they are already dominant (Wahren et al. 2005; Hudson and Henry 2009; Zamin et al. 2014).

Models incorporating both herbivory and climate change predict that in a warming climate, evergreen shrubs will have an advantage over more palatable and widely consumed deciduous shrubs such as willows where vertebrate herbivores are abundant (Yu et al. 2011). However, there is growing evidence that herbivores reduce the biomass of evergreen shrubs via indirect and direct pathways. Grazing and trampling by reindeer or caribou and browsing by small mammals reduces the height, cover, and biomass of the evergreen shrub *V. vitis-ideae*, even though it is not a preferred forage species (Pajunen *et al.*, 2008; Olofsson *et al.*, 2009, 2014; Zamin & Grogan, 2012; Table 5-2). Similarly, the biomass of *Empetrum hermaphroditum*, an

evergreen shrub usually avoided by vertebrate herbivores, was reduced by small mammals, reindeer, and to a greater extent by geometrid moth outbreaks over a fourteen year period in northern Sweden (Kaarlejärvi *et al.*, 2013; Table 5-1). Furthermore, evergreen shrubs were decimated on an island with high population density of voles, but thrived when voles were at moderate densities (Dahlgren et al. 2009). Two possible explanations for why herbivores reduce the biomass of unpalatable evergreen shrubs are A) irruptive herbivores such as voles and lemmings feed on them at population peaks when preferred foods are limited (Dahlgren et al. 2009; Olofsson et al. 2014) and B) although shoot mortality is low, the removal of even a small amount of tissue can be extremely detrimental to ericoid shrubs because inherently slow growth rates are not sufficient to replenish stored reserves in an environment where resources are often limited (Pajunen et al. 2008; Dahlgren et al. 2009). Nevertheless, exclosure studies show that herbivores reduce the height and cover of evergreen species such as *V. vitis-vitae* to a lesser extent (2-3%) than willows (3-10%; den Herder et al. 2008; Pajunen et al. 2008; Kitti et al. 2008; Table 5-2).

There is substantial evidence that the growth and distribution of non-resinous dwarf birch (*B. nana nana*) are severely limited by herbivores (Bryant *et al.*, 2014), which dampen its response to warming and fertilization (Pajunen *et al.*, 2008; Post & Pedersen, 2008; Olofsson *et al.*, 2009, 2013; Cahoon *et al.*, 2012; Table 5-1). For example, Olofsson et al. (2009) documented a 70% reduction in biomass of this shrub when exposed to vole and reindeer herbivory (Table 5-2). Conversely, resinous dwarf birch (*B. nana exilis*) may not be as strongly limited by herbivores due to the toxic triterpenes that deter herbivores (Bryant et al. 1989; Bryant et al. 2014). Evidence from an exclosure study in northern Alaska supports this idea: *B. nana exilis* growth

was greater outside than inside exclosures, and this was thought to be due to a competitive advantage over more palatable species in the presence of herbivores (Gough *et al.*, 2007; Table 5-2). *B. nana exilis* responds positively to warming and nutrient addition due to its ability to increase the number of active meristems and produce long shoots under optimal conditions (Bret-Harte et al. 2001). This sub-species' ability to both defend itself with chemically-laden resins and respond quickly to improved conditions predispose it to be one of the leaders of shrub expansion in the Arctic.

Similar to *B. nana exilis*, *B. glandulosa* is a resinous birch that is expected to be minimally influenced by herbivores (Bryant et al. 2014). *B. glandulosa* is known to respond favorably to both warming and fertilization (Zamin and Grogan 2012; Zamin et al. 2014), and therefore is likely to exploit warmer temperatures. However, evidence indicates that caribou, when present in high numbers, can dramatically reduce the biomass and prevent the recovery of birch for several years (Henry & Gunn, 1991; Manseau *et al.*, 1996; Crete & Doucet, 1998; Zamin & Grogan, 2012; Table 5-1). When herbivores were experimentally excluded, *B. glandulosa* new shoot biomass increased by 17% (Zamin and Grogan 2013; Table 5-2). *B. glandulosa* is capable of compensatory growth, producing equal amounts of aboveground biomass as un-browsed plants in response to moderate herbivory (Champagne et al. 2012). However, under heavy browsing pressure by caribou, *B. glandulosa* under-compensates (Champagne et al. 2012) and recovers much more slowly from herbivory than *Salix richardsonii* ssp. *lanata* (Henry and Gunn 1991). In Nunavik, Canada, *B. glandulosa* has undergone a marked expansion over the past half-century (Tremblay et al. 2012), which has been dampened in areas of high caribou density (Plante et al. 2014).

With its high growth rate and formidable chemical arsenal against herbivores, *Alnus viridis fruticosa* is uniquely positioned to take advantage of a warming Arctic climate. The paleo-record indicates that alder quickly spread in the early Holocene as temperatures warmed and moisture increased with the retreat of the glaciers (Oswald et al. 1999; Brubaker et al. 2005; Naito and Cairns 2011). Over the past century, alder has thrived in northern Alaska, Canada, and Siberia, and its expansion appears to be linked to warming, increased precipitation, permafrost thaw, fire frequency, and nutrient availability (Sturm et al. 2001; Tape et al. 2006; Lantz et al. 2010; Tape et al. 2012; Frost and Epstein 2014). No evidence can be found to support the idea that herbivores limit alder expansion in the Arctic, although periodic insect outbreaks (Hendrickson et al. 1991; Mulder et al. 2008), small mammals, and snowshoe hares (this study) may regulate its growth (Figure 5-3, Table 5-1). Similar to what has occurred in boreal ecosystems (Butler and Kielland 2008), herbivores may foster alder expansion by consuming competing shrub species.

Willows are expected to respond rapidly to a warming climate, but are also thought to be more strongly inhibited by herbivores than other shrubs, due to their high palatability (Bryant et al. 1989; Chapin et al. 1996). Evidence supports both predictions: willow growth and reproduction in the Arctic are limited by climate (Walker 1987; Pajunen 2009; Forbes et al. 2010) and herbivory (Berg *et al.*, 2008; den Herder *et al.*, 2008; Kitti *et al.*, 2008; Pajunen *et al.*, 2008; Ravolainen *et al.*, 2011, 2014; Cahoon *et al.*, 2012; Christie *et al.*, 2014a; Table 5-1). For example, in northern Alaska, ptarmigan browsed 82-89% of feltleaf willows (*S. alaxensis*), removing over a third of the buds and substantially altering the architecture of these shrubs (Christie *et al.*, 2014a; Figure 5-2). Furthermore, exclosure studies show that herbivores reduce

the height and cover of willows to a greater extent than other species (Table 5-2). However, willows have shown remarkable resilience to herbivory and can compensate by producing longer, larger-diameter shoots (Molvar et al. 1993; Bowyer and Neville 2003; Christie et al. 2014a). Nutrient subsidies via the feces and urine of herbivores (Ruess et al. 1989) and changes to carbon and nitrogen partitioning within plant tissues (Holland and Detling 1990) facilitate compensatory growth.

The degree to which herbivores regulate willow expansion in the Arctic will be a function of species-specific tolerance to herbivore damage, browsing intensity, and the rate at which conditions improve for willows. Perhaps the best evidence can be gleaned from long-term studies of shrub expansion. Willows have expanded over the past half-century in northern Alaska and Russia (Sturm et al. 2001; Tape et al. 2006; Walker et al. 2009; Villarreal et al. 2012). In the Russian Arctic, willow growth closely tracked regional temperatures over a 60 year period, despite the presence of reindeer herds (Forbes et al. 2010). Collectively, observational data suggest that in most locations herbivores moderate, but do not prevent the expansion of willows.

In summary, it is likely that evergreen ericoid shrubs will continue to have an advantage at less productive sites (for example, sites underlain by continuous permafrost), and are expected to respond favorably to climate change in these areas. Trampling and herbivory by vertebrates are likely to slow the expansion of this group; nevertheless, both the top-down effects of moderate herbivory and bottom-up effects of climate appear to be weaker on evergreen ericoid shrubs than for deciduous shrubs (Figure 5-4a, Table 5-3). Deciduous shrubs such as alder and willows appear to be leading the expansion of shrubs in Arctic tundra ecosystems (Sturm et al. 2001;

Tape et al. 2006; Frost and Epstein 2014). These species will respond favorably to increased disturbance frequency, longer growing seasons, permafrost thaw, and enhanced nutrient availability in the Arctic (Figure 5-4b,c). Exclosure and observational studies demonstrate that herbivores dampen the response of willows and *B. nana nana* to improved conditions in the Arctic (Figure 5-4c), whereas better-defended species such as *B. nana exilis* and *Alnus viridis* are only slightly moderated by herbivores and may be expanding more rapidly due in part to higher rates of herbivory on more palatable species (Figure 5-4b). Interestingly, during the late glacial transition (ca. 16,000–11,000 cal. yr BP) *B. nana exilis* and *Alnus viridis* dominated the positive response of vegetation to increased temperatures in the Northern Hemisphere (Kokorowski et al. 2008). Herbivore density will influence the response of shrubs to improved conditions in the Arctic such that at low herbivore densities, deciduous shrubs will respond more quickly to improved conditions than evergreen shrubs (Table 5-3). At medium herbivore densities, palatable deciduous shrubs will be targeted by herbivores allowing un-palatable deciduous and evergreen shrubs to flourish (Dahlgren et al. 2009). At high herbivore densities, the expansion of all three groups will be inhibited because herbivores are less selective (Table 5-3).

5.7 Climate change, herbivore populations, and trophic feedbacks

Herbivore populations in the Arctic are likely to change with shifting vegetation composition and phenology, increased temperatures and precipitation, longer growing seasons, and increased fire frequency and severity. Tundra specialists may over time become replaced by species better adapted to boreal conditions, as shrubs expand and sub-Arctic vegetation becomes more prevalent (Callaghan et al. 2004). Although Arctic vegetation can be remarkably resilient to tundra fires (Bret-Harte et al. 2013), increased fire severity in the Arctic is expected to decrease

winter habitat for caribou by up to 30%, but increase moose habitat by 19-63% (Joly et al. 2012). Already, caribou and reindeer have experienced declines in many parts of their ranges due to anthropogenic factors and climate change (Vors and Boyce 2009; Festa-Bianchet et al. 2011), whereas moose (*Alces alces)* and hares (*Lepus americanus, Lepus europaeus)* appear to be expanding northwards (Norment, 1999; Jansson & Pehrson, 2007; Schmidt *et al.*, 2009), consistent with model predictions (Rempel, 2011). Ptarmigan, who use willows for food and cover from predators, may benefit in the short-term from shrub expansion, and their distribution is strongly linked to the amount of shrubs exposed above the snow (Christie et al. 2014b). However, warm winters may counteract this effect and have adverse effects on Arctic ptarmigan populations by lowering the quality of subnivian roost sites and increasing the probability of rain events (Wang *et al.*, 2002).

As Arctic specialists retreat northward and boreal species expand into a more hospitable Arctic, trophic interactions are likely to change. For example, herbivores and their predators may or may not co-migrate to Arctic regions (Van der Putten et al. 2010). Snowshoe hares and moose will have strong top-down effects on expanding shrubs as they colonize parts of the Arctic, and there may be a lag before existing (*Canis lupus*) or expanding populations of predators (*Lynx canadensis)* reach sufficient densities to regulate these herbivores. Herbivore damage is much more severe where predators are absent (Dahlgren et al. 2007; Hoset et al. 2014), and expanding boreal herbivores may exhibit strong top-down control of shrubs before their population growth is regulated by predators.

5.8 Conclusion

Herbivores may play a strong role in regulating the growth and reproduction of Arctic shrubs. The variation in palatability within the shrub community translates to strong preferences (and subsequent damage) by herbivores for palatable deciduous shrubs over evergreen shrubs, although the latter can be vulnerable to trampling and herbivory where there are high concentrations of herbivores. Evidence from long-term observational and experimental studies indicates that herbivores moderate but do not prevent the expansion of fast-growing deciduous shrubs such as willows and dwarf birch. The well-defended Siberian alder is generally not preferred by herbivores and may outpace the expansion of more palatable willows. This species has the potential to substantially alter biogeochemical cycles due to its high nitrogen fixation potential (Anderson et al. 2004, Mitchell and Ruess 2009). Expanding populations of boreal herbivores consume large quantities of deciduous shrubs and will play an increasing role in moderating their expansion. For example, snowshoe hares are capable of consuming up to 80% of *Betula glandulosa* twigs during population peaks (Smith et al. 1988), and moose consume 43% of shrub biomass in areas of high density (Seaton et al. 2011).

To better understand how shrub communities, herbivore populations, and trophic interactions in the Arctic are expected to change, we suggest the following research directions:

1) Species-specific changes to shrub height, biomass, and community composition need to be monitored over the long-term to determine rates at which different species of shrubs are expanding.

2) Herbivore exclosures need to be maintained over the long-term across a broad range of Arctic habitat types to capture the effects of both expanding and eruptive species and should be designed to differentially exclude herbivores of different sizes.
3) Changes to Arctic herbivore and predator populations and their interactions need to be documented using established wildlife monitoring techniques.
4) Studies need to monitor the expansion of alder and its important role in Arctic ecosystems.

Arctic ecosystems are experiencing unprecedented change, and we must consider top-down control by herbivores as a critically important process as we attempt to understand and model these changes.

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5.10 Supporting Information

Browsing surveys took place in June 2012 along the Dalton Highway and Noatak River in northeastern and northwestern Alaska, respectively. At five sites along the Noatak River and five sites along the Dalton Highway (primarily associated with the Sagavanirktok River), three 30-m transects were established perpendicular the river. The first transect was placed in a random

location with respect to the shrub patch, and subsequent transects were placed at 50 m intervals. Shrubs were sampled at 5, 15, and 25 m along each perpendicular transect. At each sampling point, all shrub species within a 5 m radius were identified. For each species, we randomly selected 5 branches and measured evidence of browsing (yes or no), browser (hares, moose, ptarmigan, small mammal), buds browsed (ptarmigan only), buds remaining, and diameter at the point of browse (mammals only). We distinguished among browsers based on the unique marks left on the branch and the diameter at the point of browse. Ptarmigan left scars where buds had been removed, moose left ragged edges and typically consumed branch tips > 2 mm in diameter, and hares left a clean diagonal cut on the branch. We assumed that when only a small amount of branch tips (<2 mm) was removed, small mammals were responsible.

5.11 References

Anderson MD, Ruess RW, Uliassi DD, Mitchell JS (2004) Estimating N-2 fixation in two species of *Alnus* in interior Alaska using ecetylene reduction and N-15(2) uptake. Ecoscience 11: 102-112.

Batzli G, Sobaski S (1980) Distribution, abundance and foraging patterns of ground squirrels near Atkasook, Alaska. Arct Alp Res 12:501–510.

Batzli GO, Lesieutre C (1991) The influence of high quality food on habitat use by Arctic microtine rodents. Oikos 60:299–306.

Berg TB, Schmidt NM, Hoye TT, et al. (2008) High arctic plant-herbivore interactions under climate influence. Advances in Ecological Research 40: 276–298.

Bowyer RT, Neville JA (2003) Effects of browsing history by Alaskan moose on regrowth and quality of feltleaf willow. Alces 39:193–202.

Bret-Harte MS, Mack MC, Goldsmith GR, et al. (2008) Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. J Ecol 96:713–726. doi: 10.1111/j.1365-2745.2007.0

Bret-Harte MS, Mack MC, Shaver GR, et al. (2013) The response of Arctic vegetation and soils following an unusually severe tundra fire. Philos Trans R Soc Lond B Biol Sci. doi: 10.1098/rstb.2012.0490

Bret-Harte MS, Shaver GR, Zoerner JP, et al. (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. Ecology 82:18–32.

Brubaker LB, Anderson PM, Edwards ME, Lozhkin AV. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. J Biogeogr 32:833–848. doi: 10.1111/j.1365-2699.2004.01203.x

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368.

Bryant JP, Joly K, Chapin FS, et al. (2014) Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? Ecography 37:204–211. doi: 10.1111/j.1600-0587.2013.00436.x

Bryant JP, Kuropat P (1980) Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. Annu Rev Ecol Syst 11:261–285.

Bryant JP, Swihart RK, Reichardt PB, Newton L (1994) Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. Oikos 70:385–395.

Bryant JP, Tahvanainen J, Sulkinoja M, et al. (1989) Evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. Am Nat 134:20–34.

Burns KC (2014) Are there general patterns in plant defence against megaherbivores? Biol J Linn Soc 111:38–48. doi: 10.1111/bij.12181

Butler LG, Kielland K (2008) Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. J Ecol 96:136–144. doi: 10.1111/j.1365-2745.2007.0

Cahoon SMP, Sullivan PF, Post E, Welker JM (2012) Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. Glob Chang Biol 18:469–479. doi: 10.1111/j.1365-2486.2011.02528.x

Callaghan T V, Björn LO, Chernov Y, et al. (2004) Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. Ambio 33:404–417.

Champagne E, Tremblay J-P, Côté SD (2012) Tolerance of an expanding subarctic shrub, *Betula glandulosa*, to simulated caribou browsing. PLoS One 7:e51940. doi: 10.1371/journal.pone.0051940

Chapin FS, Bret-Harte SM, Hobbie SE (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. J Veg Sci 7:347–358. doi: 10.2307/3236278

Chapin FS, Shaver GR, Giblin AE, et al. (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Christie K, Ruess R, Lindberg MS, Mulder C (2014a) Herbivores influence the growth, reproduction, and morphology of a widespread Arctic willow. PLoS One 9:e101716. doi: doi:10.1371/journal.pone.0101716

Christie KS, Lindberg MS, Ruess RW, Schmutz JA (2014b) Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. Polar Biol. doi: 10.1007/s00300-014-1504-z

Clausen, TP, Bryant, JP, Reichardt PB (1986) Defense of winter-dormant green alder against snowshoe hares. Journal of Chemical Ecology 12: 2117-2131.

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899.

Crete M, Doucet GJ (1998) Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. Arct Alp Res 30:126–132.

Dahlgren J, Oksanen L, Oksanen T, et al. (2009) Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. Evol Ecol Res 1189–1203.

Dahlgren J, Oksanen L, Sjödin M, Olofsson J (2007) Interactions between gray-sided voles (*Clethrionomys rufucanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. Oecologia 152:525–32. doi: 10.1007/s00442-007-0664-8

Danell K, Bergström R, Edenius L (1994) Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. J Mammal 75:833–844.

Daniëls FJ, de Molenaar JG, Chytrý M, Tichý L (2011) Vegetation change in Southeast Greenland? Tasiilaq revisited after 40 years. Appl Veg Sci 14:230–241. doi: 10.1111/j.1654-109X.2010.01107.x

Díaz AS, Hodgson JG, Thompson K, et al. (2004) The plant traits that drive ecosystems : Evidence from three continents. J Veg Sci 15:295–304.

Elmendorf SC, Henry GHR, Hollister RD, et al. (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15:164–75. doi: 10.1111/j.1461-0248.2011.01716.x

Festa-Bianchet M, Ray JC, Boutin S, et al. (2011) Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can J Zool 89:419–434. doi: 10.1139/Z11-025

Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. Glob Chang Biol 16:1542–1554. doi: 10.1111/j.1365-2486.2009.02047.x

Fornara DA, Du Toit JT (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. Ecology 88:200–9.

Förster N, Ulrichs C, Zander M, et al. (2010) Factors influencing the variability of antioxidative phenolic glycosides in *Salix* species. J Agric Food Chem 58:8205–10. doi: 10.1021/jf100887v

Fox JF, Bryant JP (1984) Instability of the snowshoe hare and woody plant interaction. Oecologia 63:128–135.

Frost G V, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Glob Chang Biol 20:1264–77. doi: 10.1111/gcb.12406

Gough L, Moore JC, Shaver GR, et al. (2012) Above-and belowground responses of Arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. Ecology 93:1683–94.

Gough L, Ramsey EA, Johnson DR (2007) Rapid , landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Oikos 116:407–418. doi: 10.1111/j.2007.0030-1299.15449.x

Graglia E, Julkunen-tiitto R, Shaver GR, et al. (2001) Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. New Phytol 151:227–236.

Guillet C, Bergstrom R (2006) Compensatory growth of fast-growing willow (*Salix*) coppice in response to simulated large herbivore browsing. Oikos 1:33–42.

Hakkarainen H, Virtanen R, Honkanen JO, Roininen H (2007) Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biol 30:619–624. doi: 10.1007/s00300-006-0221-7

Hansen AH, Jonasson S, Michelsen A (2006) Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. Ecophysiology 147:1–11. doi: 10.1007/s00442-005-0233-y

Heiska S, Tikkanen O-P, Rousi M, Julkunen-Tiitto R (2007) Bark salicylates and condensed tannins reduce vole browsing amongst cultivated dark-leaved willows (*Salix myrsinifolia*). Chemoecology 17:245–253. doi: 10.1007/s00049-007-0385-9

Hendrickson Q, Fogal WH, Burgess D (1991) Growth and resistance to herbivory in N -fixing alders. Can J Bot 69:1919–1926.

Henry GHR, Gunn A (1991) Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic 44:38–42.

Hobbie SE, Chapin FS III (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. Ecology 79: 1526-1544.

den Herder M, Virtanen R, Roininen H (2008) Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic Appl Ecol 9:324–331. doi: 10.1016/j.baae.2007.03.005

Hilbert ADW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Hjältén J, Danell K, Ericson L (2004) Hare and vole browsing preferences during winter. Acta Theriol (Warsz) 49:53–62.

Hjältén J, Palo T (1992) Selection of deciduous trees by free ranging voles and hares in relation to plant chemistry. Oikos 63:477–484.

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Hoset KS, Kyrö K, Oksanen T, et al. (2014) Spatial variation in vegetation damage relative to primary productivity, small rodent abundance and predation. Ecography 37:001–008. doi: 10.1111/ecog.00791

Hudson J, Henry G (2009) Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90:2657–2663.

Hudson JMG, Henry GHR, Cornwell WK (2011) Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. Glob Chang Biol 17:1013–1021. doi: 10.1111/j.1365-2486.2010.02294.x

Iason GR, Palo RT (1991) Effects of birch phenolics on a grazing and a browsing mammal - a comparison of hares. J Chem Ecol 17:1733–1743.

Jansson G, Pehrson Å (2007) The recent expansion of the brown hare (*Lepus europaeus*) in Sweden with possible implications to the mountain hare (*L. timidus*). Eur J Wildl Res 53:125–130. doi: 10.1007/s10344-007-0086-2

Joly K, Duffy PA, Rupp TS (2012) Simulating the effects of climate change on fire regimes in Arctic biomes: implications for caribou and moose habitat. Ecosphere 3:1–18.

Jonasson S, Bryant JP, Iii FSC, et al. (1986) Plant phenols and nutrients in relation to variations in climate and rodent grazing. Am Nat 128:394–408.

Jung HG, Batzli GO, Seigler DS (1979) Long-term experiments reveal strong interactions between lemmings and plants in the Fennoscandian highland tundra. Biochem. Syst. Ecol. 7:203-209.

Kaarlejärvi E, Baxter R, Hofgaard A, et al. (2012) Effects of warming on shrub abundance and chemistry drive ecosystem-level changes in a forest – tundra ecotone. Ecosystems 15:1219–1233. doi: 10.1007/s10021-012-9580-9

Kaarlejärvi E, Eskelinen A, Olofsson J (2013) Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. Funct Ecol 27:1244–1253. doi: 10.1111/1365-2435.12113

Kitti H, Forbes BC, Oksanen J (2008) Long- and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biol 32:253–261. doi: 10.1007/s00300-008-0526-9

Kokorowski HD, Anderson PM, Sletten RS, Lozhkin AV, Brown TA (2008) Late glacial and early holocene climatic changes based on a multiproxy lacustrine sediment record from northeast Siberia. Arctic, Antarctic, and Alpine Research 40:497-505.

Kuropat PJ (1984) Foraging behavior of caribou on a calving ground in northwestern Alaska. University of Alaska Fairbanks

Lantz TC, Gergel SE, Henry GHR (2010) Response of green alder (*Alnus viridis* subsp . *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. J Biogeogr 37:1597–1610. doi: 10.1111/j.1365-2699.2010.02317.x

Larter NC, Nagy JA (1999) Seasonal changes in the composition of the diets of Peary caribou and muskoxen on Banks Island. Polar Res 23:131–140.

Manseau M, Huot J, Crete M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. J Ecol 84:503–513.

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161.

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886.

Mitchell JS, Ruess RW (2009) N-2 fixing alder (*Alnus viridis* spp. *fruticosa*) effects on soil properties across a secondary successional chronosequence in interior Alaska. Biogeochemistry 95:215-229.

Molvar EM, Bowyer RT, Van Ballenberghe V, Van Brauenberone V (1993) Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479.

Montgomerie R, Holder K (2008) Rock Ptarmigan (*Lagopus muta*). Birds North Am Online. doi: doi:10.2173/bna.51

Mulder CPH (1999) Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities, and ecosystems. Perspect Plant Ecol Evol Syst 2:29–55. doi: 10.1078/1433-8319-00064

Mulder CPH, Roy B., Güsewell S (2008) Herbivores and pathogens on *Alnus viridis* subsp. *fruticosa* in Interior Alaska: effects of leaf, tree, and neighbour characteristics on damage levels. Botany 86:408–421. doi: 10.1139/B08-015

Myers-Smith IH, Forbes BC, Wilmking M, et al. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:610–623. doi: 10.1088/1748-9326/6/4/045509

Naito AT, Cairns DM (2011) Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. Environ Res Lett 6:045506. doi: 10.1088/1748-9326/6/4/045506

Nilsson M-C, Gallet C, Wallstedt A (1998) Temporal of phenolics variability and batatasin-III in *Empetrum hermaphroditum* leaves over an eight-year period: interpretations of ecological function. Oikos 81:6–16.

Norment CJ (1999) Important bird and mammal records in the Thelon River valley, Northwest Territories: Range expansions and possible causes. Can Field-Naturalist 113:375–385.

Olofsson J, Beest M, Ericson L (2013) Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. Philos. Trans. R. Socie 368: 20120486

Olofsson J, Oksanen L, Callaghan T, et al. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. Glob Chang Biol 15:2681–2693. doi: 10.1111/j.1365-2486.2009.01935.x

Olofsson J, Oksanen L, Oksanen T, et al. (2014) Long-term experiments reveal strong interactions between lemmings and plants in the Fennoscandian highland tundra. Ecosystems 17:606–615. doi: 10.1007/s10021-013-9740-6

Oswald WW, Brubaker LB, Anderson PM (1999) Late Quaternary vegetational history of the Howard Pass area , northwestern Alaska. Can J Bot 77:570–581.

Pajunen A, Virtanen R, Roininen H (2008) The effects of reindeer grazing on the composition and species richness of vegetation in forest–tundra ecotone. Polar Biol 31:1233–1244. doi: 10.1007/s00300-008-0462-8

Pajunen AM (2009) Environmental and biotic determinants of growth and height of Arctic willow shrubs along a latitudinal gradient. Arctic, Antarct Alp Res 41:478–485. doi: 10.1657/1938-4246-41.4.478

Palo R (1985) Chemical defense in birch: inhibition of digestibility in ruminants by phenolic abstracts. Oecologia 68:10–14.

Paragi T, Seaton T, Kellie K (2008) Identifying and evaluating techniques for wildlife habitat management in interior Alaska: moose range assessment. Final Research Technical Report. Grants W-33-4, 5, 6 and 7. Project 5.10. Juneau

Pedersen S, Andreassen HP, Persson I, et al. (2011) Vole preference of bilberry along gradients of simulated moose density and site productivity. Integr Zool 6:341–351. doi: 10.1111/j.1749-4877.2011.00260.x

Pérez-Harguindeguy N, Díaz S, Vendramini F, et al. (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. Austral Ecol 28:642–650. doi: 10.1046/j.1442-9993.2003.01321.x

Plante S, Champagne E, Ropars P (2014) Shrub cover in northern Nunavik: can herbivores limit shrub expansion? Polar Biol 37:611–619. doi: 10.1007/s00300-014-1461-6

Pomeroy JW, Bewley DS, Essery RLH, et al. (2006) Shrub tundra snowmelt. Hydrol Process 20:923–941. doi: 10.1002/hyp.6124

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci U S A 105:12353–12358. doi: 10.1073/pnas.0802421105

Predavec M, Danell K (2001) The role of lemming herbivory in the sex ratio and shoot demography of willow populations. Oikos 3:459–466.

Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos Trans R Soc Lond B Biol Sci 365:2025–34. doi: 10.1098/rstb.2010.0037

Rammul U, Oksanen T, Oksanen L, et al. (2007) Vole vegetation interactions in an experimental, enemy free taiga floor system. Oikos 116:1501–1514. doi: 10.1111/j.2007.0030-1299.14981.x

Ravolainen VT, Bråthen KA, Ims RA, et al. (2011) Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Basic Appl Ecol 12:643–653. doi: 10.1016/j.baae.2011.09.009

Ravolainen VT, Bråthen KA, Yoccoz NG, et al. (2014) Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. J Appl Ecol 51:234–241. doi: 10.1111/1365-2664.12180

Rempel RS (2011) Effects of climate change on moose populations: Exploring the response horizon through biometric and systems models. Ecol Modell 222:3355–3365. doi: 10.1016/j.ecolmodel.2011.07.012

Ruess RW, Hik DS, Jefferies RL (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23–29.

Schmidt JI, Hundertmark KJ, Bowyer RT, McCracken KG (2009) Population structure and genetic diversity of moose in Alaska. J Hered 100:170–80. doi: 10.1093/jhered/esn076

Seaton CT, Paragi TF, Boertje RD, et al. (2011) Browse biomass removal and nutritional condition of moose *Alces alces*. Wildlife Biol 17:55–66. doi: 10.2981/10-010

Singer FJ, Mark LC, Cates RC (1994) Ungulate herbivory of willows on Yellowstone's northern winter range. J Range Manag 47:435–443.

Skarpe C, van der Wal R (2002) Effects of simulated browsing and length of growing season on leaf browsing characteristics and flowering in a deciduous Arctic shrub, *Salix polaris*. Arctic, Antarct Alp Res 34:282–286.

Smith JNM, Krebs CJ, Sinclair ARE, Boonstra R (1988) Population biology of snowshoe hares. II. Interactions with winter food plants. J Animal Ecol 57: 269-286.

Speed JDM, Austrheim G, Hester AJ, Mysterud A (2010) Experimental evidence for herbivore limitation of the treeline. Ecology 91:3414–20.

Stewart KM, Bowyer RT, Ruess RW, et al. (2006) Herbivore optimization by North American Elk: consequences for theory and management. Wildl Monogr 167:1–24.

Stokkan K, Steen JB (1980) Age determined feeding behaviour in willow ptarmigan chicks *Lagopus lagopus lagopus*. Ornis Scand 11:75–76.

Sturm M, Racine C, Tape K, et al. (2001) Increasing shrub abundance in the Arctic. Nature 411:2001–2002.

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob Chang Biol 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x

Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic Alaska. Ecosystems 15:711–724. doi: 10.1007/s10021-012-9540-4

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186–193. doi: 10.2980/17-2-3323

Tolvanen A, Schroderus J, Henry GHR (2002) Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. Evol Ecol 443–462.

Tremblay B, Lévesque E, Boudreau S (2012) Recent expansion of erect shrubs in the Low Arctic: evidence from Eastern Nunavik. Environ Res Lett 7:035501. doi: 10.1088/1748-9326/7/3/035501

Villarreal S, Hollister RD, Johnson DR, et al. (2012) Tundra vegetation change near Barrow, Alaska (1972 – 2010). Environ Res Lett 7:015508. doi: 10.1088/1748-9326/7/1/015508

Vors LS, Boyce MS (2009) Global declines of caribou and reindeer. Glob Chang Biol 15:2626–2633. doi: 10.1111/j.1365-2486.2009.01974.x

Wahren C-H, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Glob Chang Biol 11:537–552. doi: 10.1111/j.1365-2486.2005.00927.x

Walker D, Leibman MO, Epstein HE, et al. (2009) Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. Environ Res Lett 4:045004. doi: 10.1088/1748-9326/4/4/045004

Walker D (1987) Height and growth rings of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska. Botany 65:988–993. doi: 10.1139/b87-136

Walker MD, Wahren CH, Hollister RD, et al. (2006) Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci U S A 103:1342–6. doi: 10.1073/pnas.0503198103

Wandera AJL, Richards JH, Mueller RJ (1992) The relationships between relative growth rate , meristematic potential and compensatory growth of semiarid-land shrubs. Oecologia 90:391–398.

Wang G, Hobbs NT, Giesen KM, et al. (2002) Relationships between climate and population dynamics of white-tailed ptarmigan *Lagopus leucurus* in Rocky Mountain. Clim Res 23:81–87.

Weeden R (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

White RG, Trudell J (1980) Habitat preference and forage consuption by reindeer and caribou near Atkasook, Alaska. Arct. Alp. Res. 12:

Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: A review and assessment of three opposing models. Am Nat 169:443–54. doi: 10.1086/512044

Wright IJ, Reich PB, Westoby M, et al. (2004) The worldwide leaf economics spectrum. Nature 428:821–7. doi: 10.1038/nature02403

Yu Q, Epstein HE, Walker D, et al. (2011) Modeling dynamics of tundra plant communities on the Yamal Peninsula, Russia, in response to climate change and grazing pressure. Environ Res Lett 6:045505. doi: 10.1088/1748-9326/6/4/045505

Zamin TJ, Bret-Harte MS, Grogan P (2014) Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra. J Ecol 102:749–766. doi: 10.1111/1365-2745.12237

Zamin TJ, Grogan P (2012) Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. Environ Res Lett 7:034027. doi: 10.1088/1748-9326/7/3/034027

Zamin TJ, Grogan P (2013) Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. J Ecol 101:671–683. doi: 10.1111/1365-2745.12082

5.12 Figures

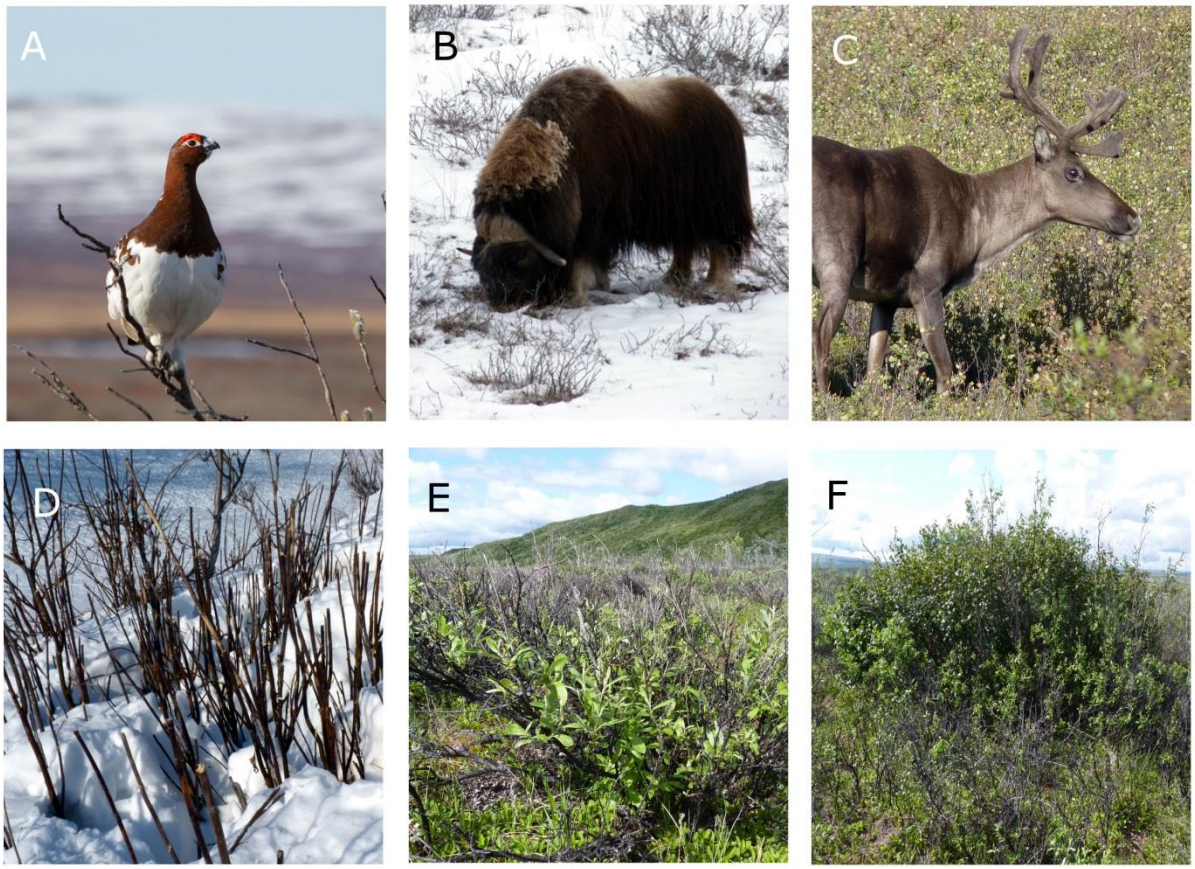

Figure 5-1. Typical Arctic herbivores: willow ptarmigan (A), muskox (B), and caribou (C); willows recently browsed by moose and ptarmigan (D), willows with canopy die-off due to browsing (E), and a healthy alder growing in an Arctic riparian floodplain with browsed willows in the foreground (F). Willow ptarmigan photo by Neil Paprocki, caribou photo by Sophie Gilbert, all others by Katie Christie.

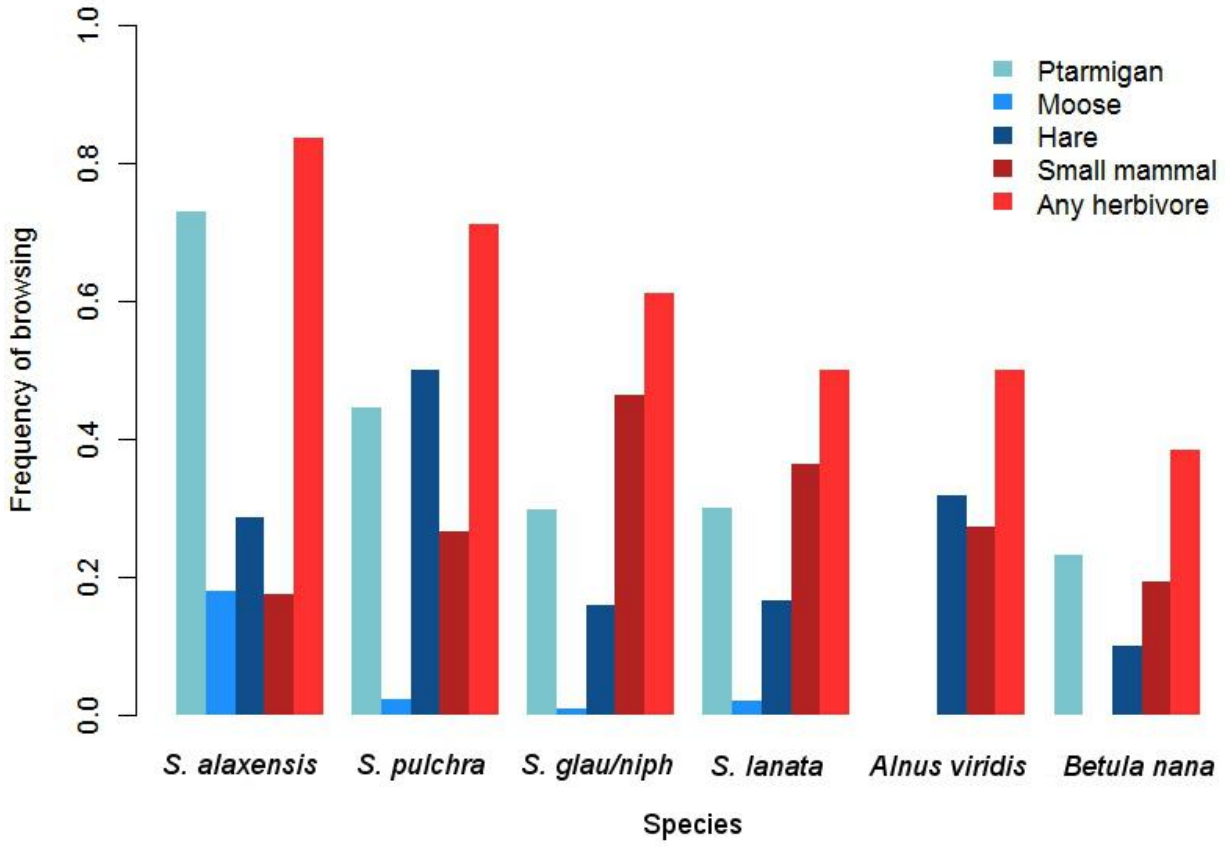

Figure 5-2. Results from browsing surveys near the Noatak and Sagavanirktok Rivers, Alaska showing the frequency of browsing (proportion of plants browsed) by different vertebrate herbivores. "S. alax" denotes *Salix alaxensis* and "S. glau/niph" denotes *Salix glauca* or *Salix niphoclada* (the two species were grouped). The last category (any herbivore) was calculated as the number of plants browsed by any herbivore divided by the total number of plants sampled for each species.

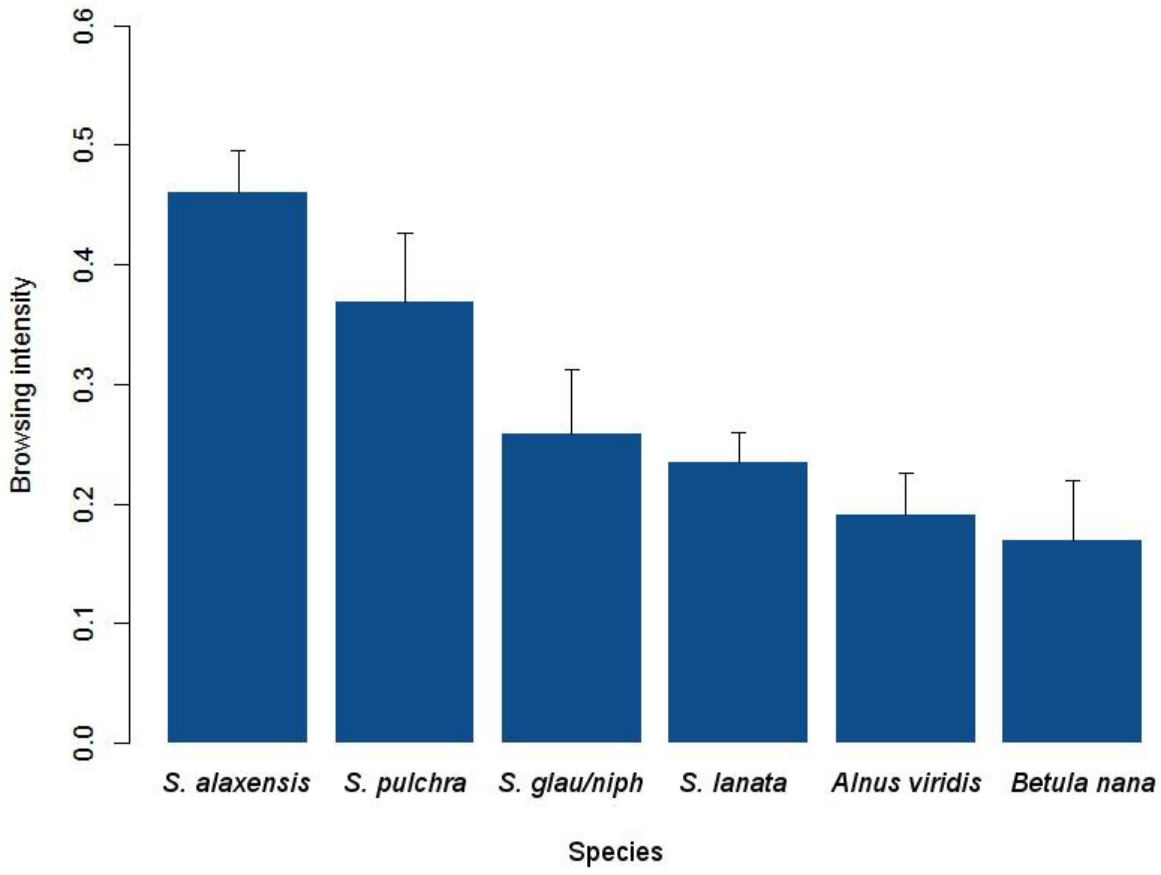

Figure 5-3. Browsing intensity (proportion of stems browsed on a plant) by all herbivores on different species of shrubs near the Noatak and Sagavanirktok Rivers, Alaska. “S. alax” denotes *Salix alaxensis* and “S.glau/niph” denotes *Salix glauca* or *Salix niphoclada* (the two species were grouped). Herbivores include moose, ptarmigan, hares, and small mammals.

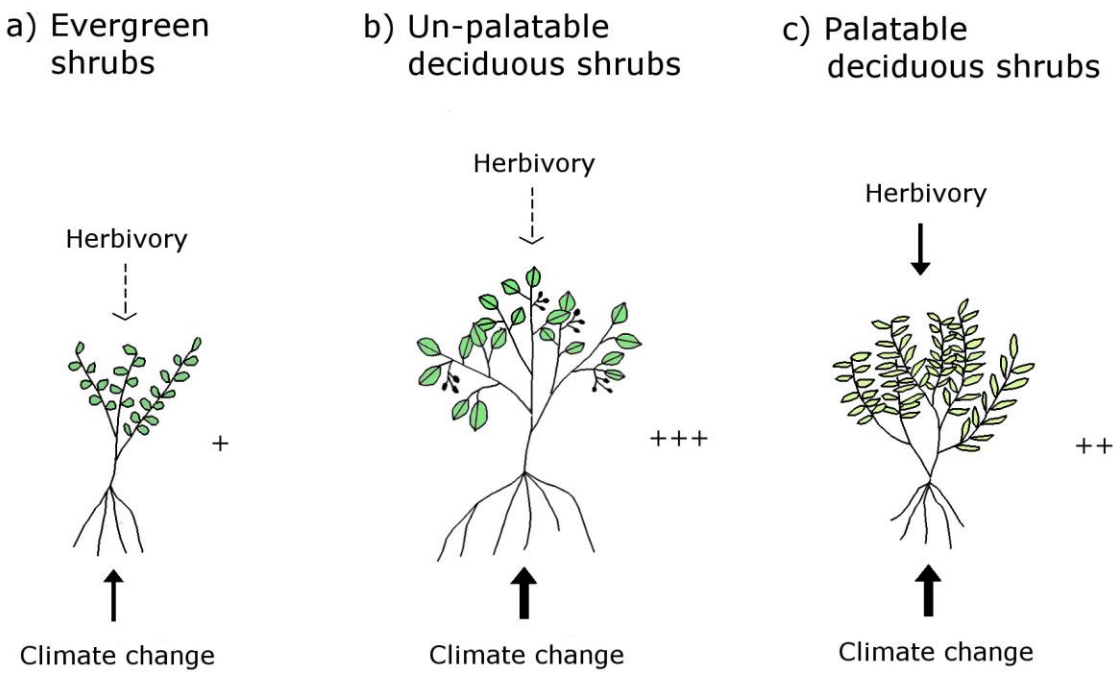

Figure 5-4. Illustration of how moderate levels of herbivory and climate change regulate different shrub groups. The thickness of arrows represents the strength of the effect, with the dashed line representing the weakest effect. The effect of climate depends on innate growth rate, response to altered conditions, and site conditions, whereas the effect of herbivory depends on palatability, browsing pressure, tolerance, and resource limitation. The plus signs reflect the net effect of top-down and bottom-up forces, where more plus signs indicate greater predicted shrub expansion.

5.13 Tables

Table 5-1. Dominant shrub species in tundra ecosystems and their principal herbivores, documented response to warming, and evidence for limitation by herbivores. Blank cells indicate that no data were available.

Shrub group	Shrub species	Region	Herbivore	Response to warming	Evidence that herbivores limit expansion	References
Evergreen shrubs	*Empetrum nigrum* ssp. *Hermaphroditum* (crowberry)	circumpolar arctic	Not preferred by reindeer, voles or ptarmigan, geese consume berries	Responded strongly to warming in forest, weekly in tundra, increased biomass in response to warming in Japan, no expansion observed in Greenland		Banfield 1974, Williams 1980, Sedinger and Raveling 1984, Kudo and Suzuki 2003, Daniëls et al. 2011, Kaarlejarvi et al. 2012
	Dryas integrifolia (Entire-leaved aven)	North America and Greenland	Arctic ground squirrel, muskox, caribou, ptarmigan	Taller shoots, larger leaves		Klein and Bay 1994, Hudson et al. 2011, Williams 1980
	Dryas octopetalia (mountain aven)	circumpolar arctic	collared lemming	Increased shoot height and leaf biomass, greater rates of photosynthesis, advanced phenology	Flowering is reduced by lemming herbivory	Berg et al. 2008
	Vaccinium vitis-idaea (lingonberry, low-bush cranberry)	circumpolar arctic	Generally not preferred by browsers. Browsed by gray-sided voles when *V. myrtillus* depleted	No effect of warming or moderate increase in cover	Grazing and trampling by caribou reduce leaf biomass, height, and cover	Chapin et al. 1995, Kudo and Suzuki 2003, Pajunen et al. 2008, Kaarlejarvi et al. 2012, Zamin and Grogan 2013

Table 5-1 (continued):

Shrub group	Shrub species	Region	Herbivore	Response to warming	Evidence that herbivores limit expansion	References
Deciduous shrubs	*Vaccinium myrtillus* (bilberry)	Fennoscandia	Mountain hares, ptarmigan, microtine rodents, gray-sided voles	No effect	Biomass strongly related to herbivory pressure. Voles can severely reduce abundance, although it recovers quickly	Stokkan and Steen 1980, Hjalten et al. 2004, Dahlgren et al. 2007, Dahlgren et al. 2009, Pedersen et al. 2011, Kaarlejarvi et al. 2012, Soininen et al. 2013
	Vaccinium uliginosum (northern bilberry, bog bilberry)	circumpolar arctic	voles, caribou, bears	Increased flower production but not biomass	Grazing of competing species by caribou enhanced the growth of this species	Banfield 1974, Zamin and Grogan 2013
	Betula nana ssp. *nana* (non-resinous dwarf birch)	Fennoscandia, Iceland, Greenland, eastern Canada	Reindeer, lemmings, muskoxen, Gray-sided voles only when *V. myrtillus* is depleted	Increased cover, increased radial and vertical growth	Biomass reduced by reindeer, voles, and lemmings	Dahlgren 2007, Pajunen et al. 2008, Post and Pedersen 2008, Olofsson et al. 2009, Olofsson et al. 2012, Kaarlejarvi et al. 2012
	Betula nana ssp. *exilis* (dwarf resin birch)	Siberia, North America	Ptarmigan, snowshoe hares (not preferred), only slightly palatable to tundra and singing voles	Increased cover and biomass	Voles and caribou did not inhibit expansion and may have indirectly enhanced expansion by removing competitors	Weeden 1969, Bryant et al. 1989, Batzli and Lesieutre 1991, Chapin et al. 1995, Wahren et al. 2005, Gough et al. 2007, Gough et al. 2012, this study

Table 5-1 (continued):

Shrub group	Shrub species	Region	Herbivore	Response to warming	Evidence that herbivores limit expansion	References
Deciduous shrubs	*Betula glandulosa* (resin birch)	North America, Greenland	Caribou, snowshoe hares (although they reject shoot tips), ptarmigan	Increased cover and apical stem growth	Heavy caribou browsing and trampling limits leaf biomass and cover. Compensates for moderate but not heavy browsing pressure. Expansion has been kept in check in areas of high caribou density	Bergerud 1972, Smith et al. 1988, Henry and Gunn 1991, Manseau et al. 1996, Crete and Doucet 1998, Champagne et al. 2012, Zamin and Grogan 2012, Tremblay et al. 2012, Liu et al. 2013, Plante et al. 2014, Zamin and Grogan 2013, Zamin et al. 2014
	Alnus viridis fruticosa (Siberian alder)	Siberia, North America	Snowshoe hares (although they reject buds),small mammals	Increased cover		Bryant et al. 1983, Hendrickson et al. 1991, Sturm et al. 2001, Tape et al. 2006, Tape et al. 2012, Lantz et al. 2013, Frost and Epstein 2014, this study
	Salix alaxensis (feltleaf willow)	North America	Snowshoe hares ptarmigan, moose, small mammals		Ptarmigan and moose limit sexual reproduction and vertical growth of this species	Bryant et al. 1989, Bowyer and Neville 2003, Christie et al. 2014, this study
	S. pulchra (diamondleaf willow)	North America, Siberia	ptarmigan, snowshoe hares, small mammals, moose	Increased cover and height		Wahren et al. 2005, Myers-Smith et al. 2011, Villareal et al. 2012, this study

Table 5-1 (continued):

Shrub group	Shrub species	Region	Herbivore	Response to warming	Evidence that herbivores limit expansion	References
Deciduous shrubs	*Salix spp.* (not differentiated)	circumpolar arctic	reindeer, caribou, moose, muskox, small mammals, hares, ptarmigan	Increased cover, height, biomass		Klein and Bay 1994, Sturm et al. 2001, Tape et al. 2006, Forbes et al. 2011
	S. phylicifolia (tea-leaved willow)	Northern Europe, Asia	Mountain hares, reindeer		Cover and height reduced by reindeer	Bryant et al. 1989, Pajunen et al. 2008
	S. glauca (gray-leaf willow)	North America, Fennoscandia, Greenland, Siberia	reindeer, tundra and singing voles, ptarmigan, moose, snowshoe hares, muskoxen	Increased cover and height	Herbivores reduce cover, height, and growth	Batzli and Lesieutre 1991, den Herder et al. 2008, Pajunen et al. 2008, Post and Pedersen 2008, Daniëls et al. 2011, Myers-Smith et al. 2011, this study
	S. arctica (arctic willow)	North America, Asia, Greenland	muskoxen, collared lemmings	Taller shoots, larger leaves	Productivity and biomass reduced by muskoxen	Tolvanen et al. 2002, Berg et al. 2008, Hudson et al. 2011
	S. laponum (downy willow)	Northern Europe	reindeer		Height and cover reduced by reindeer	Kitti et al. 2009

Table 5-2. Proportional reduction in height, cover, biomass, and shoot length from herbivore exclosure studies. Values have been standardized so that they reflect changes over the course of one year. Positive values indicate that plants had a positive response to the presence of herbivores relative to plants protected from herbivores. Each row represents a different site where exclosures were erected. Only studies that used exclosures and reported effect size were included.

	Evergreen shrubs		Resin birches		Non-resin birch	Deciduous ericoids		Willows			
	V. vitis idaea	*R. subarct-icum*	*B. nana exilis*	*B. gland-ulosa*	*B. nana nana*	*V. uglin-osum*	*V. myrt-illus*	*S. phylici-folica*	*S. lapp-onum*	*S. glauca*	Reference
Height	-0.02[a]	-	-	-	-0.01[a]	-	-	-0.07[b]	-0.03[c]	-0.05[a]	[a]Pajunen et al. 2008,[b]den Herder 2008, [c]Kitti et al. 2009
	-0.04	-	-	-	-0.01	-	-	-	-	-0.10	Pajunen et al. 2008
	-0.02	-	-	-	0.03	-	-	-	-	-0.07	Pajunen et al. 2008
	-0.02	-	-	-	-0.04	-	-	-	-	0.00	Pajunen et al. 2008
	-0.03	-	-	-	-0.01	-	-	-	-	-0.08	Pajunen et al. 2008
Mean	-0.03	-	-	-	-0.01	-	-	-0.07	-0.03	-0.06	

Table 5-2 continued

	Evergreen shrubs		Resin birches		Non-resin birch	Deciduous ericoids		Willows			
	V. vitis idaea	*R. subarct-icum*	*B. nana exilis*	*B. gland-ulosa*	*B. nana nana*	*V. uglin-osum*	*V. myrt-illus*	*S. phylici-folica*	*S. lapp-onum*	*S. glauca*	Reference
Cover	-0.01[a]	-	-	-	-0.1[a]	-	-	-0.1[a]	-0.09[b]	-0.10[a]	[a]Pajunen et al. 2008,[b]Kitti et al. 2009
	-0.04	-	-	-	0.04	-	-	-0.09	-	0.03	Pajunen et al. 2008
	-0.04	-	-	-	-0.05	-	-	-0.1	-	-0.09	Pajunen et al. 2008
Mean	-0.03	-	-	-	-0.04	-	-	-0.10	-0.09	-0.05	
Change in biomass^	0.50	-	-	-	1.40	-	-2.50	-	-	-	Olofsson et al. 2009
	-1.00	-	-	-	-0.81	-	-1.56	-	-	-	Olofsson et al. 2009
	0.00	-	-	-	-0.79	-	-1.00	-	-	-	Olofsson et al. 2009
	0.00	-	-	-	-3.00	-	0.00	-	-	-	Olofsson et al. 2009

^Change in biomass was calculated as the increase or decrease in biomass (g/m2) over the course of one year

Table 5-2 continued

	Evergreen shrubs		Resin birches		Non-resin birch	Deciduous ericoids		Willows			
	V. vitis idaea	*R. subarct-icum*	*B. nana exilis*	*B. gland-ulosa*	*B. nana nana*	*V. uglin-osum*	*V. myrt-illus*	*S. phylici-folica*	*S. lapp-onum*	*S. glauca*	Reference
Change in biomass^ continued	-1.00	-	-	-	-0.41	-	-1.25	-	-	-	Olofsson et al. 2009
	-1.00	-	-	-	-1.17	-	0.00	-	-	-	Olofsson et al. 2009
	-1.50	-	-	-	0.00	-	0.00	-	-	-	Olofsson et al. 2009
	-0.57	-	-	-	-0.80	-	-1.26	-	-	-	Olofsson et al. 2009
Mean	-0.57	-	-	-	-0.70	-	-0.95	-	-	-	
Biomass Index*	-	-	-	-	-0.09	-	-	-	-	-0.02	Post and Pedersen 2008
New stem biomass	0.00	-0.17	-	-0.17	-	0.31	-	-	-	-	Zamin and Grogan 2013

*Biomass index was calculated based on the amount of vegetation intercepted by a pin lowered from a plexiglass sheet

Table 5-2 continued

	Evergreen shrubs		Resin birches		Non-resin birch	Deciduous ericoids		Willows			
	V. vitis idaea	*R. subarct-icum*	*B. nana exilis*	*B. gland-ulosa*	*B. nana nana*	*V. uglin-osum*	*V. myrt-illus*	*S. phylici-folica*	*S. lapp-onum*	*S. glauca*	Reference
Shoot length	-	-	0.00	-	-	-	-	-	-	-	Gough et al. 2007
	-	-	-0.08	-	-	-	-	-	-	-	Gough et al. 2007
	-	-	-0.09	-	-	-	-	-	-	-	Gough et al. 2007†
	-	-	0.06	-	-	-	-	-	-	-	Gough et al. 2007†
Mean	-	-	-0.03	-	-	-	-	-	-	-	

†Plots were fertilized with nitrogen and phosphorous

Table 5-3. How different shrub groups are expected to respond to climate change under different densities of herbivores.

Herbivore density	Evergreen shrubs	Un-palatable deciduous shrubs	Palatable deciduous shrubs
Low	+	+++	+++
Medium	+	+++	++
High	-	++	+

Chapter 6

General Conclusions

The information presented in this dissertation enhances our knowledge of ptarmigan migration, habitat associations, and browsing ecology in northern Alaska. Arctic ptarmigan populations depend on tall feltleaf willow stands as a critical resource during the winter and spring, while strongly influencing their growth, reproduction, and architecture.

Ptarmigan are strongly associated with major riparian drainages where willows grow tall enough to exceed snow depth (Chapter 2). In areas with > 30% shrub cover, ptarmigan occupancy was greater than 90%, indicating that ptarmigan had a high probability of visiting and browsing these shrub patches. Ptarmigan occupancy in northern Alaska increased from early to late spring, providing evidence that they migrate from wintering grounds south of the Brooks Range to Arctic breeding grounds in the spring. In the high snow year of the study, ptarmigan occupied fewer survey units than in the moderate snow year, when more shrub habitat was available. Shrub expansion may increase habitat for ptarmigan in the near future, although over the long-term the replacement of Arctic vegetation by boreal plants (Callaghan et al. 2004) may result in overall population declines.

Feltleaf willow (*Salix alaxensis*) stands dominate the floodplains of major Arctic rivers in Alaska (Schickhoff et al. 2002) and provide important food and shelter for ptarmigan during the winter and spring (Irving et al. 1966; Irving et al. 1967; Weeden 1969). Willows are expected to respond rapidly to warmer Arctic temperatures , but this response is likely to be tempered by

herbivores (Bryant et al. 1989; Chapin et al. 1996). Ptarmigan herbivory was highly prevalent in feltleaf willow stands at study sites in northeastern and northwestern northern Alaska, where 82-89% of randomly chosen willows were browsed (Chapter 3). By removing terminal buds, ptarmigan stimulated otherwise dormant buds at the base of shoots to produce new vegetative shoots, which were twice as large and bore 40-60% more buds than shoots produced on un-browsed branches. Catkin production was reduced to near zero on browsed branches. Browsing altered the bud demographic rates (bud survival, production, transition from dormant buds to vegetative shoots), which in turn influenced plant structure and future forage availability to ptarmigan. Willows with a history of browsing (as evidenced from brooming) were shorter than un-browsed willows and had a greater chance of being re-browsed by ptarmigan. Moose-browsed willows also produced larger shoots and fewer catkins, but broomed willows were not preferred by this herbivore.

The combined results of the simulated browsing experiment and feeding preference study with wild ptarmigan (Chapter 4) provided further evidence that ptarmigan regulate willow architecture and bud production to their own advantage. Similar to what was found with wild-browsed willows, simulated ptarmigan browsing reduced catkin production, increased the numbers of buds per shoot, and altered the morphology of willow branches so that multiple live and dead shoots originated from a single origin (brooming). Although buds were 20% smaller, total bud biomass increased from 113 mg of accessible buds (between 80 and 130 cm) on un-browsed willows to 129 mg of accessible buds on browsed willows. Browsing did not induce a defensive response in feltleaf willows and instead reduced protein precipitation capacity by 20%. When broomed and un-broomed branches were placed in the snow at equal heights, ptarmigan

did not show a preference, but obtained more buds from broomed (22 ± 1.6 buds) than un-broomed branches (19 ± 1.3 buds). This lends support to the hypothesis that by pruning willows and creating browsing "hedges" in feltleaf willow stands, ptarmigan regulate their own food resource, similar to other plant-herbivore systems (McNaughton 1984; Roininen et al. 1988; Person et al. 2003; Stewart et al. 2006; Craig 2010).

The last chapter of this dissertation synthesized research on the effects of vertebrate herbivory on shrub expansion in the Arctic. Original data from northern Alaska, in combination with observational and experimental studies from across the Arctic indicate shrubs differ strongly in their palatability to herbivores, and these differences translate to variation in growth reduction by herbivores. Willows and non-resin birches are more strongly regulated by herbivores than resin birches, Siberian alder, and evergreen ericoid shrubs. Long-term studies of vegetation change show that the expansion of palatable deciduous shrubs is tempered but not prevented by herbivores. As conditions improve in the Arctic, un-palatable but fast growing species such as Siberian alder may have an advantage over more palatable species such as willows.

Herbivores have the capacity to strongly impact Arctic vegetation and therefore need to be considered when modeling future shrub expansion. In northern Alaska, one of the most important but overlooked herbivores is ptarmigan (*Lagopus lagopus, L. muta*). This research clearly demonstrates how this small but ubiquitous Arctic bird substantially alters the reproduction and morphology of riparian willows across a wide spatial scale.

6.1 References

Bryant JP, Tahvanainen J, Sulkinoja M, et al. (1989) Evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. Am Nat 134:20–34.

Callaghan T V, Björn LO, Chernov Y, et al. (2004) Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. Ambio 33:404–417.

Chapin FS, Bret-Harte SM, Hobbie SE (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. J Veg Sci 7:347–358. doi: 10.2307/3236278

Craig TP (2010) The resource regulation hypothesis and positive feedback loops in plant–herbivore interactions. Popul Ecol 52:461–473. doi: 10.1007/s10144-010-0210-0

Irving L, West C, Peyton LJ, Paneak S (1966) Migration of willow ptarmigan in arctic Alaska. Arctic 20:77–85.

Irving L, West GC, Peyton LJ (1967) Winter feeding program of Alaska willow ptarmigan shown by crop contents. Condor 69:69–77.

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886.

Person BT, Herzog MP, Ruess RW, Sedinger JS (2003) Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592. doi: 10.1007/s00442-003-1

Roininen H, Price PW, Tahvanainen J (1988) Field test of resource regulation by the bud-galling sawfly, *Euura mucronata*, on *Salix cinerea*. Holarct Ecol 11:136–139. doi: 10.1111/j.1600-0587.1988.tb00791.x

Schickhoff U, Walker MD, Walker DA (2002) Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. Phytocoenologia 32:145–204. doi: 10.1127/0340-269X/2002/0032-0145

Stewart KM, Bowyer RT, Ruess RW, et al. (2006) Herbivore optimization by North American Elk: consequences for theory and management. Wildl Monogr 167:1–24.

Weeden R (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.